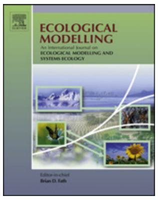
Ecological Modelling 222 (2011) 935–946

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



Large scale parameter study of an individual-based model of clonal plant with volunteer computing

C. Mony[a,*], M. Garbey[b], M. Smaoui[b], M.-L. Benot[a]

[a] UMR CNRS 6553 ECOBIO, Univ. Rennes 1, Av. General Leclerc, 35042 Rennes Cedex, France
[b] Dept. Computer Sciences, Univ. Houston, 01 Philip G. Hoffman Hall, Houston, TX 77204-3010, USA

ARTICLE INFO

Article history:
Received 18 February 2010
Received in revised form 5 October 2010
Accepted 14 October 2010

Keywords:
Volunteer computing
Individual-based model
Plant performance
Plant clonal strategies
Multiparameter method

ABSTRACT

Understanding clonal strategies (i.e. the ability of plants to reproduce vegetatively) is particularly important to explain species persistence. A clonal individual may be considered as a network of interconnected ramets that colonizes space. Resources in this network can be shared and/or stored. We developed an individual-based model (IBM) to simulate the growth of an individual clonal plant. Typically a realistic IBM requires a large set of parameters to adequately represent the complexity of the clonal plant growth. Simulations in the literature are often limited to small subsets of the parameter space and are guided by the a priori knowledge and with heuristic aims of the researcher. The aim of this paper was to demonstrate the benefit of volunteer computing in computational ecology to systematically browse the parameter space and analyze the simulation results in order to draw rigorous conclusions. To be specific, we simulated clonal plant growth using nine growth rules related to the metabolic process, plant architecture, resource sharing and storage and nineteen input parameters. We chose 2–4 values per input parameter which corresponded to 20 millions of combinations tested through volunteer computing. We used three criteria to evaluate plant performance: plant total resource, ramet production and maximum length of one branch. The 1% top-performing plants were sorted according to these criteria. Plant total resource and ramet production were correlated while considering the top-performing plants. The maximum length of one branch was independent from the other two performance traits. We detected two processes promoting at least one of the plant performance traits: (i) a relatively high metabolic gain (high photosynthetic activity and low production cost for new growth units), a low resource storage and long integration distance for resource sharing; (ii) short spacer lengths and the predominance of elongation of existing branches over branching. Interactive effects between parameter values were demonstrated for more than half of the input parameters. Best performance was reached for plants with slightly different combinations of values for these parameters (i.e. different strategies) rather than a single one (i.e. unique strategy). This modeling approach with volunteer computing enabled us to proceed to large-scale virtual experiments which provided a new quality of insight into ecological processes linked with clonal plant growth.

1. Introduction

Clonality is widespread among herbaceous plants. Up to 70–80% of the species in some plant communities are able to reproduce by cloning (Klimeš et al., 1997). Cloning for a plant consists of developing a network of potentially autonomous shoots (ramets) connected by horizontal modified shoots (connections), either under or above ground. These connections often lack chlorophyll and do not contribute significantly to plant photosynthesis. This form of reproduction enables plants to colonize space (Hutchings and Mogie, 1990; Stöcklin and Winkler, 2004). The relationships between plant clonal growth patterns and individual performance are particularly determinant in understanding the dynamics of plant communities.

In clonal plants, growth patterns are constrained by different processes related to (i) plant architecture (Wildovà et al., 2007) which governs ramet spacing, branching frequency and angle (Sintes et al., 2005) directly determining the spatial position of ramets, (ii) resource translocation: photoassimilates may indeed be translocated between ramets over a certain distance (Hutchings and Bradbury, 1986; Jónsdóttir and Watson, 1997) and/or stored in connections and at the basis of shoots (Huber and Stuefer,

---

* Corresponding author. Tel.: +33 2 23 23 64 79.
E-mail addresses: cendrine.mony@univ-rennes1.fr (C. Mony), garbey@cs.uh.edu (M. Garbey), msmaoui@cs.uh.edu (M. Smaoui), marie-lise.benot@univ-rennes1.fr (M.-L. Benot).

0304-3800/$ – see front matter © 2010 Elsevier B.V. All rights reserved.
doi:10.1016/j.ecolmodel.2010.10.014

1997; Turner and Pollock, 1998), and (iii) intra-individual plasticity. Plastic adjustments of ramet morphology and clonal architecture improve the foraging capacity of plants (de Kroon and Hutchings, 1995; McLellan et al., 1997). These processes can largely determine how plant communities are structured in space and time (Klimeš et al., 1997) as they should determine plant performance. Plant performance in clonal plants is difficult to evaluate due to their hierarchical organization: from ramets to genets (Winkler and Fischer, 1999). Plant growth rate (i.e. the rate at which an individual is growing) is usually taken into account for estimating plant performance (Fagerström, 1992; Wikberg, 1995) but in clonal plants, performance may also correspond to the production of ramets (i.e. potential future new plants) or the ability to colonize space (Sackville-Hamilton et al., 1987). Space colonization promotes the placement of new ramets in favorable sites (Bell, 1984) or the competitiveness of the plant (Herben and Hara, 1997). Therefore we hypothesize that performance is best evaluated by these complementary indicators.

Analyzing the effect of plant architecture or resource translocation and storage on plant performance is difficult to address through experimentation. Modeling, on the other hand, can be a useful tool for providing a realistic formulation of plant growth. Clonal growth has been modeled using different spatially explicit models (see reviews by Sutherland and Stillman, 1990; Oborny and Cain, 1997). Among those, individual-based models (IBMs) have been recognized to be of particular interest (Winkler and Klotz, 1997; Herben and Suzuki, 2001; Kun and Oborny, 2003). Plant horizontal growth was modeled as from simple spatial diffusion rates to highly complex patterns of clonal properties. Realistic IBMs require however a large set of parameters to adequately represent the complexity of the clonal plant dynamic. As far as we know, simulation experiments in the literature are often limited to small subsets of the parameter space and are guided by the a priori knowledge and heuristic of the researcher. The number of simulations is also restricted by evaluating the effect of these parameters on plant performance through varying only one parameter at a time or by calculating only one criterion of plant performance, generally plant biomass. From a complex discrete stochastic dynamical system such as the IBM of clonal plant growth, one may expect multiple coupling between various mechanism for architecture or metabolism that are difficult to study with this approach.

The aim of this paper was to demonstrate the benefit of volunteer computing in computational ecology to systematically browse the parameter space and analyze the simulation results. Volunteers are typically members of the general public who own Internet-connected PCs and provide computing resources to projects. The first project using volunteer computing started in 1996 (Great Internet Mersenne Prime Search), followed by others such as SETI@home and Folding@home (Anderson et al., 2002). Contributions were made to the development of volunteer computing platforms such as BOINC (Berkeley Open Infrastructure for Network Computing) (Anderson, 2004), which comprises nowadays more than 50 projects in all disciplines. The present article is part of the Virtual Prairie (ViP) project relaid by the website http://vcsc.cs.uh.edu/virtual-prairie that gathers several thousands of PCs of volunteers. This is up to our knowledge the first project in ecology using volunteer computing (Garbey et al., 2008).

We developed our own individual-based model (IBM) to simulate the growth of an individual clonal plant. The design of our model is not fundamentally original, since many other IBMs have been tested in the literature. We referred to Sutherland and Stillman (1990) and Oborny and Cain (1997) for extensive reviews on the topic. The computational approach presented in this paper can be applied to any of these models. To be specific our individual clonal plant growth was simulated using nine growth rules related to the metabolic process, resource sharing and storage and plant architecture. We tested the effect of sixteen out of the nineteen input parameters implemented in the model on plant performance traits. We chose 2–4 values per parameter and tested therefore 20 millions of parameter value combinations. We concentrated our plant performance evaluation on three criteria: plant total resources, ramet production and maximum length of one branch. Our goal with our IBM model was to:

i. detect clonal traits contributing to plant performance and the correlations between performance output parameters. We focused on traits linked with architectural and resource translocation,
ii. analyze plant strategies under optimal conditions of growth (i.e. undisturbed, without competition nor resource stress)

2. Model description

2.1. Purpose

A clonal plant was simulated as a network of ramet units connected by connection units forming branches (Fig. 1). The state variable of this cellular automaton describes the location of ramets and connection units in the cells of an hexagonal grid. Short-term growth of an individual clonal plant was simulated (only one season). No ramet mortality or sexual birth was therefore included. In parallel we have set up a semi-controlled experiment with individual clonal plants (Benot et al., 2009). While there is not enough data available to validate rigorously our IBM, our observations suggested that a ramet unit may correspond to a cell of diameter of approximately two centimeters and should be produced at a maximum speed of one per day. We used therefore a 99 by 99 hexagonal grid so that no plant could reach the border in the time of the simulation. A cell is uniquely defined by its coordinates with the couple of integers $(x,y); x, y \in \{1...99\}$. We chose an hexagonal grid rather than a rectangular grid as it gives more realistic simulations of the competitive interaction between ramets, simpler calculation of distance and orientation of growth process and clarity when visualized (see Birch et al., 2007 for a review). Using regular grids is less realistic than free-grid CA as it does not allow continuous interval of orientation for branching (see Berger et al., 2008 for a review), but it makes a very simple assumption on the maximum density of ramets allowed that can be related to our experiments.

This model includes properties linked with plant metabolism, resource integration and architecture. We aimed at modeling a wide range of clonal plants. There are however the following restrictions: the model takes into account only plants: (1) with rhizomes and non-photosynthetic stolons, (2) that develops into network structures (no tussock species), (3) that cannot adjust plastically along the developmental stages. The ecological limits of these choices are discussed further.

2.2. Scales

The model comprises four different scales defined to take into account the particular properties of clonal plants. Variables for each scale are described in Table 1. We used the following scales:

- *The growth unit* (connection (c) or ramet (r)): Ramets and connections may differ in two main functions: (i) nutrient uptake and resource synthesis and (ii) resource storage. We assumed that ramet units contributed to the uptake of nutrients and synthesis of resources through their well-developed roots and photosynthetic organs (feeding sites, *sensu* Bell, 1984), while connections did not. These resources may be available for immediate growth or be used for long-term reserve formation, which corresponds

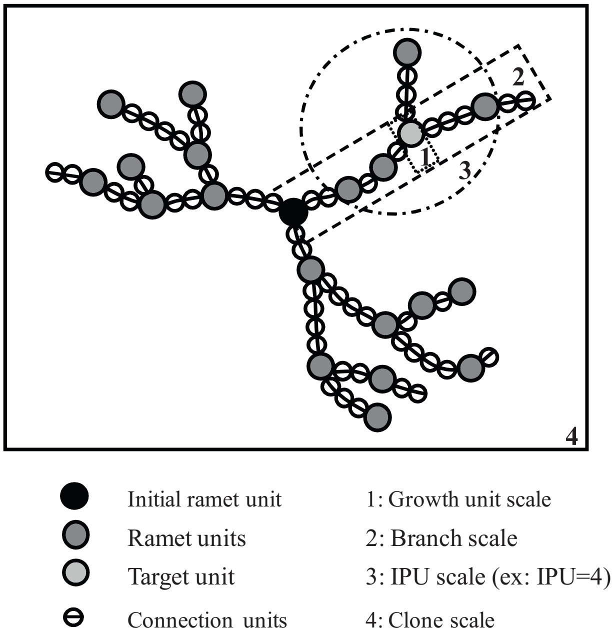


Fig. 1. General architecture of a clonal plant and illustrations of the different scales of processes involved in plant growth.

to the synthesis of storage substances at the expense of immediate growth (Chapin et al., 1990). In clonal plants, connections often specialize in long-term resource storage (Steen and Larsson, 1986; Hartnett, 1989; Suzuki and Stuefer, 1999; Asaeda et al., 2006). We assumed therefore that connection units were able to store resources that are not required for short-term growth (i.e. long-term reserves), while ramet units were not. Variables linked with each growth unit are the quantity of resource accumulated (R_g with g being a ramet r or a connection c) and the probability of creating a new growth unit (p_r or p_c) for a ramet and a connection unit respectively. Each ramet may be further associated with a distance to the origin of the branch (d(r)). The probability of branching (p_{br}(r)) depends on the growth rules described below.

- *The branch* (*b*) (a series of interconnected ramets belonging to the same branch). A branch is composed of at least two ramets interconnected by multiple connection units representing the spacer. We define the spacer length *D* as the number of connection units constituting the spacer. New branches may be created from a ramet unit. We gave each branch a generation number *G*(b) (1: primary branch, 2: secondary branch i.e. branching from a primary branch, 3: tertiary branch i.e. branching from a secondary branch) and a length *L*(b) calculated as the total number of consecutive units (both connection and ramet units) of the branch. Each branch can be associated with a probability to elongate (P_{el}(b)) or to branch (P_{br}(b)) depending on the growth rules described below.
- *The integrative physiological unit* (*IPU*) (the number of consecutive units where resource translocation and sharing occur, Watson, 1986). The integration distance within the network may vary from one spacer to the whole clone (Klimeš et al., 1997). Integration generally supports active growth parts of the clone (Kelly, 1995): either young ramets (Marshall, 1990; Price et al., 1992; Alpert, 1996) or branch extremities (Landa et al., 1992; Price and Hutchings, 1992; D'Hertefeldt and Jónsdóttir, 1999) in order to provide resources for creating new growth units. We assumed that integration did not depend on the developmental stage of the units of the IPU. IPU is associated with an amount of resource available for new growth (R_{IPU}) and to an amount of resource stored ($R_{s\text{-}IPU}$).
- *The clone* (T) (whole set of ramets and connection units). We associated with the clone T the following variables: total amount of resources (R_T), total number of ramets (n_T) and plant spatial extension defined as the length of the longest branch among the clone (L_{Tm}).

2.3. Model framework

The model is a stochastic discrete dynamical system driven by a decision tree where each node corresponds to a category of actions, for example elongation, branching or creation of a ramet. For each generic action A, we assumed that the model obeys the probability law: above a certain threshold the action is fulfilled; below, it is not. In the absence of detailed knowledge of the clonal pro-

Table 1
List of the variables of the model.

Name	Law	Significance
t		Time
x, y		Spatial coordinates of one cell over the grid
$D(x,y)$	(L4)	Spacer length for the cell (x, y)
Growth unit scale		
g		A growth unit (it is denoted c when it is a connection, r, when it is a ramet)
R_g	(L1)–(L3)	Resource of the growth unit g
p_{br}(r)	(L8)	Probability of branching of the ramet r
d(r)	(L8)	Number of growth units between the basis of the branch and the ramet r
Branch scale		
b		A branch
G(b)	(L6)–(L7)	Generation number of the branch b
L(b)	(L6)–(L7)	Length of the branch b
p_{el}(b)	(L6)	Probability of elongation of the branch (b)
p_{br}(b)	(L7)	Probability of branching of each branch (b)
IPU scale		
R_{IPU}	(L3), (L9)	Resource of the IPU available for new growth
$R_{s\text{-}IPU}$		Resource of the IPU stored
Clone scale		
T		A clone
n_T		Number of ramets of the clone
R_T	(L1)	Resource of the clone
L_{Tm}		Length of the longest branch among the clone
$p_{el/br}$	(L5)	Probability to elongate
p_g	(L9)	Probability of creating the new growth unit
$\mu, \alpha, \beta, \gamma, \delta, \varepsilon$	(L4)–(L9)	Random variables expressing stochasticity

cess, we used generic linear first order dependence. We also used multiplication rules when there was more than one control variable providing therefore the independence of these variables. For instance, if x and y are control variables used in the decision process to realize the action A, the probability law is computed such as $p=(a_1+b_1x)(a_2+b_2y)$. All units have an equiprobability to realize action A if b_1 and b_2 are equal to 0. Otherwise, they will depend more or less strongly on variables x or y depending on the values of b_1 and b_2. This probability is calculated for all units that are potentially involved in supporting action A: this applies for instance to all branches apex for the action which is the elongation of the branch (depending on the length and the generation number of the branch which are the two control variables) or to all ramets within an existing branch for the action of branching (depending on the location of this ramet along the branch which is the control variable). The unit with the highest probability is selected among those for action A. For convenience we skipped the normalization needed to keep p in the range [0,1], as the highest value for the probability of the event is selected. In the following we denoted random variables in the interval [0,1] by greek letters.

2.4. Model variables

Plant growth patterns are dependent on processes ruled with (L1)–(L9) and the parameters listed in Table 2.

2.4.1. Plant metabolism and resource storage

Resource of the clone depends on plant metabolism and resource strategy. We allow the creation of no more than one new ramet or connection unit per time step. The energy cost C for the creation of a new ramet unit ($C=c_r$) may differ from the cost of a new connection unit ($C=c_c$). Globally the total resource of the clone denoted $R_T(t)$ evolves in time t following:

$$R_T(t+1)=R_T(t)+\sum_{g=1}^{g=n}R_g(t)-aC \quad t\in[1,100]$$

from an initial condition that corresponds to a unique isolated

$$\text{ramet of initial biomass } R_T(1)=1 \tag{L1}$$

where R_T is the resource status of the clone, $R_g(t)$ is the net gain of resource (either by accumulation for ramets or by storage for connection units)at time t for the growth unit g, $C$is the production cost of one growth unit (c_c or c_r). In this equation a is zero if no unit has been added, one otherwise.

In (L1), maintenance costs for ramets are included in the calculation of the net resource uptake r_p whereas they are neglected for connections. Each ramet in the network produces a certain amount of resources (r_p) i.e. net resource uptake which is split in a fraction r_s to long-term reserve formation allocated to the preceding spacer and $(1-r_s)$ to short-term resource available for growth. Long-term reserve is allocated equally among the connection units of the preceding spacer. The accumulation of short-term resources was made at the ramet level and was assumed to be dependent on its existing biomass, the increase in resource decreasing with the size. It was therefore modeled as a logistic law following the work of Gardner and Mangel (1999). We assumed that a ramet r cannot accumulate more than a certain amount of resources r_m:

$$\frac{dR_r(t)}{dt}=r_p(1-r_s)R_r(t)\left(1-\frac{R_r(t)}{r_m}\right) \tag{L2}$$

where $R_r(t)$ is the resource status (short-term resource accumulation) at the time t for ramet r, r_p is the resource uptake by one ramet for one time step (per unit of time), r_s the fraction of resources allocated to long-term reserve formation, r_m the maximum resource accumulated in the ramet. r_m was fixed to 20. This value was chosen from a controlled experiment where 10 clonal fragments of the rhizomatous Cyperacea *Carex divisa* Huds. were grown in undisturbed conditions in the experimental garden of the University of Rennes 1. We assumed ramet height to be a good indicator of the resource status of a ramet. The height of a ramet per clonal fragment was monitored from its birth during 12 weeks. Maximum height was reached for most ramets between 35 and 42 days (unpubl. results). We fixed therefore r_m in order that $R_r(t)$ reached its maximum value within this range of time steps. Resource available for growth for a given ramet r is calculated over all the growth units of the IPU following (L3):

$$R_{\mathrm{IPU}}(r)=\sum_{i=1}^{i=n_{\mathrm{IPU}}}R_i \tag{L3}$$

where R_i is the resource of the growth unit i, n_{IPU} is the number of growth units of the IPU. R_i is equal to 0 for a connection unit which stores only long-term resource unavailable for growth.

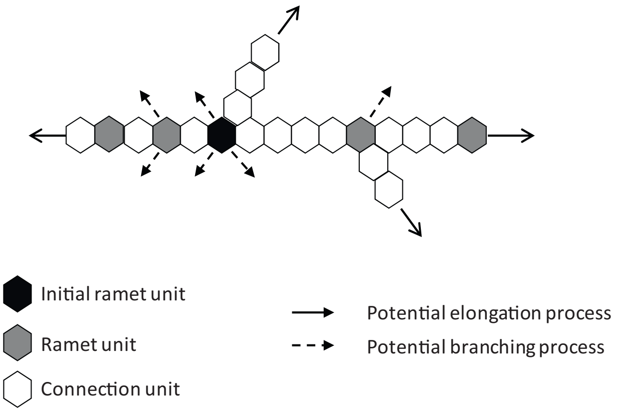


Fig. 2. Potential locations of the elongation/branching processes, taking the example of a simulation ($n_0=6$; $n_b=2$).

2.4.2. Plant form and spatial colonization

Plant architecture is basically determined by the available number of buds at each node and their activation through spatial colonization processes. Colonization of space is achieved by two processes: through the elongation of existing branches (elongation process) or the creation of new branches at a ramet node (branching process) (Fig. 2). Both processes depends on the spacer length.

Because once a ramet is created, it will stay until the end of the season (no mortality within a season), we computed a priori once and for all the spacer length $D(x,y)$ for each cell (x,y) of the hexagonal grid. Each cell of the grid is therefore associated with a value of spacer length. The spacer developing from a given ramet has the length corresponding to the value that was calculated and attributed to the cell occupied by this ramet. Spacer lengths attributed to cells that are not occupied by ramets are not used. $D(x,y)$ follows a stochastic law (L4):

$$D(x,y)=d_0+\mu d_1,\ \mu\in[0;1] \tag{L4}$$

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

The minimum spacer length is d_0 and the maximum is (d_0+d_1). Consequently, the spacer length may vary randomly among the clone.

The location of the new growth unit within the clone was selected after two subsequent modeling steps: (i) the choice of the process for colonizing space, elongation or branching; (ii) the choice of the branch that will support this new growth unit and its location along the branch selected (only for the branching process).

The first step (elongation vs. branching) is achieved following (L5):

$$p_{\mathrm{el/br}} = \alpha \quad \alpha \in [0;1] \tag{L5}$$

where $p_{\mathrm{el/br}}$ is the probability to elongate, α is a random variable in the range 0–1 and $p_{\mathrm{el/br(0)}}$ is the threshold value for elongation vs. branching process. If $p_{\mathrm{el/br}} > p_{\mathrm{el/br(0)}}$, this is an elongation process whereas if $p_{\mathrm{el/br}} \leq p_{\mathrm{el/br(0)}}$, it is a branching process.

This trade-off simulates the architectural range between phalanx (highly ramified, short branches) to guerilla (few but long branches) types (Schmid and Harper, 1985).

The second step (potential location of the new growth unit (connection or ramet)) depends on the order (G(b)) and length (L(b)) of the branches within the clone.

For the elongation process, the probability of elongation of each branch was calculated following (L6):

$$p_{\mathrm{el}}(\mathrm{b}) = \beta \frac{1}{(1 + E_l G(\mathrm{b}))(1 + E_g L(\mathrm{b}))} \quad \beta \in [0;1] \tag{L6}$$

where p_{el} (b) is the probability of elongation of each branch (b), β is a random variable in the range 0–1, G(b) and L(b) the generation number and the length of the branch respectively. E_l and E_g expresses the dependence of elongation on the generation number and length of the branch respectively.

If E_l is high, the branch with the lowest generation number will have the highest probability to elongate whereas if E_g is high, the branch with the lowest length will elongate. The elongation extends the branch in the same direction.

For the branching processes, the location of the new growth unit is selected in function of the branch and the ramet unit along this branch which have the highest probability to branch. The probability of branching of each connection (p_{br}) is calculated following (L7):

$$\begin{aligned} p_{\mathrm{br}}(\mathrm{b}) &= \gamma \frac{(1 + B_l L(\mathrm{b}))}{(1 + B_g G(\mathrm{b}))} \quad \gamma \in [0;1[\quad \mathit{if}\ G(\mathrm{b}) < 3 \\ p_{\mathrm{br}}(\mathrm{b}) &= 0 \qquad\qquad\qquad\qquad\quad \mathit{if}\ G(\mathrm{b}) \geq 3 \end{aligned} \tag{L7}$$

where p_{br} (b) is the probability of branching of each branch (b), γ is a random variable in the range 0–1, G(b) and L(b) the generation number and the length of the branch respectively. B_l and B_g expresses the dependence of branching on the generation number and length of the branch respectively.

If B_l is high, the branch with the longest length will branch whereas if B_g is high, the branch with the lowest generation number will branch. The probability of creating a new growth unit at each ramet node along the connection (p_{r}) is calculated following (L8):

$$p_{\mathrm{br}}(\mathrm{r}) = \delta \frac{1}{e(1 + B_{\mathrm{p}} d(\mathrm{r}))} \quad \delta \in [0;1] \tag{L8}$$

where p_{br}(r) is the probability of branching of each ramet (r) along the branch, δ is a random variable in the range 0–1, e is a constant, d(r) is the distance (expressed as the number of growth units) between the ramet r considered and the basis of the branch it belongs to. B_p expresses the dependence of the branching process on the distance of the ramet to the basis of the branch.

If B_p is high, ramets located close to the branch basis will have the highest probability to branch.

The number of branches produced from a ramet unit depends on the activation of buds available. Branching from the parent ramet unit corresponds to the production of primary connections. It can occur in six directions (0°, 60°, 180°, 120°, 240°, 300°) and depends on the number of buds n_0. Angle 180° points out to the direction toward the basis of the branch while 0° points out to its apex. For secondary branching, we restrict ourselves to forward branching, i.e. we use only two possible directions (60°, 300°) in the limit of the number of buds imposed by the parameter n_{b}. Rules (L6)–(L8) were implemented in the model to simulate a range of plant architecture from strongly age-dependent architecture to unorganized architecture.

2.5. The updating process

As discussed earlier, the model proceeds in daily time steps (t). Each simulation starts with a ramet unit at the center of the hexagonal grid. Since we allow branches to cross at the level of connection units, each cell of the grid could be empty or occupied by a ramet unit or several connection units or occupied by a ramet unit and several connection units. In the software we maintain a dual representation of the clone with the hexagonal grid for space distribution and a tree structure for the topology of connections. Within each time step, four phases are processed in the following order:

- *Calculation of resource*: Each ramet produces r_{p}, allocated to short-term storage (L2) and long-term storage (r_{s}). Long-term storage is a percentage of the resource uptake r_{p} of the ramet.
- *Calculation of the location of the potential new growth unit*: This calculation is a function of the branching vs. elongation processes (L5). Once the event (elongation or branching) is determined (L5), the location of the newly created growth unit depends on the probability (L6) if the event is an elongation and on the probabilities (L7) and (L8) if the event is branching. The cell having the highest probability of becoming a new growth unit is selected.
- *Calculation of the type of the new growth unit*: If the event is an elongation, the type of the new growth unit – either connection or ramet – is defined in relation to the spacer length value D attributed to the last ramet along the branch: if the distance from the last ramet is lower than this spacer length, it becomes a connection unit; otherwise a ramet unit is produced. If the event is branching, a connection unit is created.
- *Calculation of the probability of creating the new growth unit*: The resource balance is analyzed within the IPU corresponding to the potential placement of the new growth unit. The probability of a new growth unit (p_g) being created depends on the ratio of resources available within the IPU vs. the cost of producing the growth unit following (L9):

$$\begin{aligned} p_g &= \varepsilon \left[1 + \log\left(\frac{R_{\mathrm{IPU}}}{c_g}\right)\right] \quad \text{with}\ \varepsilon \in [0;1] \quad \text{if}\ R_{\mathrm{IPU}} \geq c_g \\ p_g &= 0 \qquad\qquad\qquad\qquad\qquad\qquad\quad \text{if}\ R_{\mathrm{IPU}} < c_g \\ & \qquad p_g = p_{\mathrm{r}}\ \text{or}\ p_{\mathrm{c}} \\ & \qquad c_g = c_{\mathrm{r}}\ \text{or}\ c_{\mathrm{c}} \end{aligned} \tag{L9}$$

where p_g is the probability of creating the new growth unit, ε is a random variable in the range 0–1, R_{IPU} is the available resources within the IPU and c_{r} and c_{c} are the production cost of one ramet and one connection unit respectively. The growth unit is created if $p_g > p_{g0}$.

Ramet units are created only in grid cells not yet occupied by a ramet, whereas connection units may be created in empty or occupied cells. This simple rule simulates intraclonal competition between ramets. If the cell for the placement of the new ramet unit is already occupied, it is not created and a new time step begins. If the growth unit is created, the IPU is depleted of the amount of resources that was necessary to create the growth unit (c_{r} or c_{c} for a ramet or a connection unit respectively). At each time step, only one growth unit is created on the whole clone even if the amount of resources available is sufficient to support the creation of further units.

Table 2
List of the input parameters of the model: 16 among 19 parameters were tested in the model.

Significance	Label	Values
Plant metabolism and resource storage		
Energy increment per time step per ramet unit (L2)	r_{p}	0.3; 0.15; 0.07
Energy allocated to reserve formation in connection units	r_{s}	0; 0.1; 0.4
Energy cost for the creation of a ramet unit (L1)	c_{r}	1
Energy cost for the creation of a connection unit (L1)	c_{c}	0.02; 0.5; 0.8
Maximum resource accumulated for a ramet unit (L2)	r_{mr}	20
Maximum resource stored for a connection unit (L2)	r_{mc}	10
Threshold probability for the creation of a new growth unit (L9)	p_{g0}	0.4; 0.6; 0.8
Number of growth units of the IPU (L3)	n_{IPU}	1; 5; 10; 50
Plant form and spatial colonization		
Maximum number of branches developing from the initial ramet	n_0	2; 4; 6
Maximum number of branches developing from ramets other than the initial ramet	n_{b}	1; 2
Minimum spacer length between two ramets (L4)	d_0	1; 2; 3; 4
Variability in the spacer length (L4)	d_1	0; 2
Threshold probability for the elongation process (L5)	$p_{\mathrm{el/br(o)}}$	0.2; 0.5; 0.8
Dependence of elongation on the length of the branch (L6)	E_l	0.02; 0.2; 2
Dependence of elongation on the generation number of the branch (L6)	E_g	0.001; 0.01; 0.1
Dependence of branching on the length of the branch (L7)	B_l	0.001; 0.01; 0.1
Dependence of branching on the generation number of the branch (L7)	B_g	0.02; 0.2; 2
Constant in (L8)	a	0; 1
Dependence of the branching location on the distance of the ramet to the basis of the branch (L8)	B_p	0.001; 0.01; 0.1

2.6. Simulations

Simulations were stopped after 100 time steps. This choice of the number of time steps gave a significant percentage, among all parameter combinations tried, of clones with a number of branches and ramets comparable to the best performances we recorded in our semi-controlled experiment. A higher number of time steps may require the implementation of mechanism such as ramet senescence or competition to be realistic.

Nineteen input parameters were introduced in the model: 16 were tested and 3 were fixed (Table 2). We selected two to four values for each parameter: these values covered a wide range of clonal plants within the restriction detailed at the beginning of the method section. These values were selected arbitrary based on our heuristic knowledge of clonal plants without any precise calibration on real plants. We calculated three output parameters related to plant performance (Liao et al., 2003; Puijalon et al., 2005). These were (A) plant total resource, which was approximated from the sum of resources stored both short-term and long-term in the network; (B) future new plants by the number of ramets (each ramet can potentially give another plant if disconnected from the others); (C) plant spatial extension, estimated from the length of the longest branch.

The IBM obeys a given number of probabilistic rules. One simulation is therefore meaningless. Indicators of the performances of the clone were therefore computed for many replicates with the same input parameter set. We computed average as well as standard deviation of these indicators with a sufficient number of replicates to insure that the imperfect convergence of this Monte–Carlo method did not affect our conclusions. For precaution we over-estimated this number and used 1000 replicates. Systematic simulations were made for all combinations of the values tested of the 16 input parameters (i.e. 22,674,816 combinations) and the mean and standard deviation of the three output parameters were calculated for 1000 replicates of each of these combinations of values. These 22,674,816,000 clones were simulated through volunteer computing using the BOINC platform.

The BOINC middleware is project based. These academic projects (university-based) are independently run and maintained. BOINC has a server/client architecture where the server handles work generation, distribution and aggregation. The clients on the other hand which are the volunteered computation resources, typically internet connected personal computers owned by individuals all over the world, achieve the actual simulations. We established at first a list of all combinations of parameters to be tested. One BOINC job corresponds to the 1000 replicated simulations using the same input parameter combination picked from the 22,674,816 different combinations. The jobs were processed in a random order of the parameter combinations. The BOINC server sends jobs at the request of the clients in a first-arrived, first-served basis: the server treats the request of the clients sequentially. In order to avoid wrong answers linked with malicious users or defective PCs, we issued for each BOINC job two replicates (twin jobs). Each one of the twin jobs was sent to a different client. The results of the two clients were compared and accepted if they matched. We fixed a fairly strict tolerance based on a convergence assumption for the result comparison, such that when the difference between the mean of the 1000 runs for both twin jobs was above that tolerance, a third identical job was reissued to confirm either of the results. We are able to monitor the activity of our clients and to spot the systems that give either slow or wrong answers. We have also a number of clients that are actually part of the computing resources of our University center for computing. Those are by definition non-malicious system that we can rely on, if needed. The BOINC software comes with customizable tools that allow us to choose our scheduling, redundancy and result validation policies.

2.7. Data analysis

Data analyses for such large database were not trivial. All the results were gathered in a matrix format. We created three different matrixes taking into account only plants (i.e. simulations) which performed the best according to the output parameters *A*, *B* and *C*. The corresponding matrices denoted [*A*], [*B*] and [*C*] comprised the plants which had the top 1% performance according to the output parameters *A*, *B* and *C* respectively. Our findings were not very sensitive to that specific percentage: we tested 0.3% and 3% top percentage and obtained results consistent with the one detailed below (data not shown). Each matrix had a dimension of 226,748 lines (corresponding to the 1% of the simulations) and 22 columns corresponding to the 16 parameters tested in the model (input parameters, Table 2) and the mean and standard deviation over 1000 replicates of the three performance traits calculated on the plant at the end of the simulation (output parameters *A*, *B* and *C*).

For each matrix [*A*], [*B*] and [*C*], we analyzed: (1) how plants were distributed among the set of values chosen for each input parameter and (2) the correlations between the resulting output parameters. These analyses aimed at detecting the combination of input traits that performed the best for one of the three criteria selected.

(1) In order to analyze which input parameters determine plant performance; we calculated for each of them the number of plants for the set of values tested. To analyze the result we classified the input parameters into three different categories:
   (i) sensitive parameter with a single optimum: parameters where more than 90% of plants corresponded to one of the values tested (*unique value parameters*),
   (ii) unsensitive parameters with no obvious optimum value: parameters where plants were equally distributed between the values of the input parameter (*equi-distributed parameters*). We considered that plants were equally distributed between the different values of the parameter when the number of plants for each value of the parameter was in a range of: $\left[100/n(0-0,1);100/n(1+0,1)\right]$ where n is the number of values tested for the parameter. An equi-distributed parameter was hence when plants were distributed between 45% and 55% for both values for a 2-category parameter, 30–37% for all values for a 3-category parameter and 22–28% for all values for a 4-category parameter,
   (iii) sensitive parameters with complex control: parameters where plants were distributed unevenly between the different values of the input parameter (*complex distributed parameters*).

   Unique value parameters were determinant in plant performance whereas equi-distributed parameters did not impact plant performance within the range of values tested. We assumed that the occurrence of complex distributed parameters indicated interactive effects between these parameters and that a combination of parameter values rather than one parameter value had an effect on plant performance. To test this idea, we computed a cluster analysis taking into account only complex-distributed parameters after centering and normalizing the matrix of parameter values. We used *k*-means clustering. This method of cluster analysis aims at partitioning *n* observations into *k* clusters in which each observation belongs to the cluster with the nearest mean (MacQueen, 1967). Euclidean distance was used as a metric and variance was used as a measure of cluster scatter. The number of clusters kretained was calculated depending on the average silhouette of the data (Rousseeuw, 1987). We used this clustering analysis for detecting the occurrence of potential groups of plants based on their combination of values for these complex distributed parameters. We calculated the percentage of plants per value for each complex distributed parameter in order to identify the set of values characterizing each cluster. To make sure that these clusters corresponded to similar performances, we calculated the mean and standard-deviation of the performance parameter for each cluster and compared them.

(2) We calculated Pearson correlations between each pair of output parameters *A*, *B* and *C*. We considered that the correlation was strong when it was higher than 0.4.

   Statistical significance of these tests was not calculated owing to the huge number of data (226,748 lines).

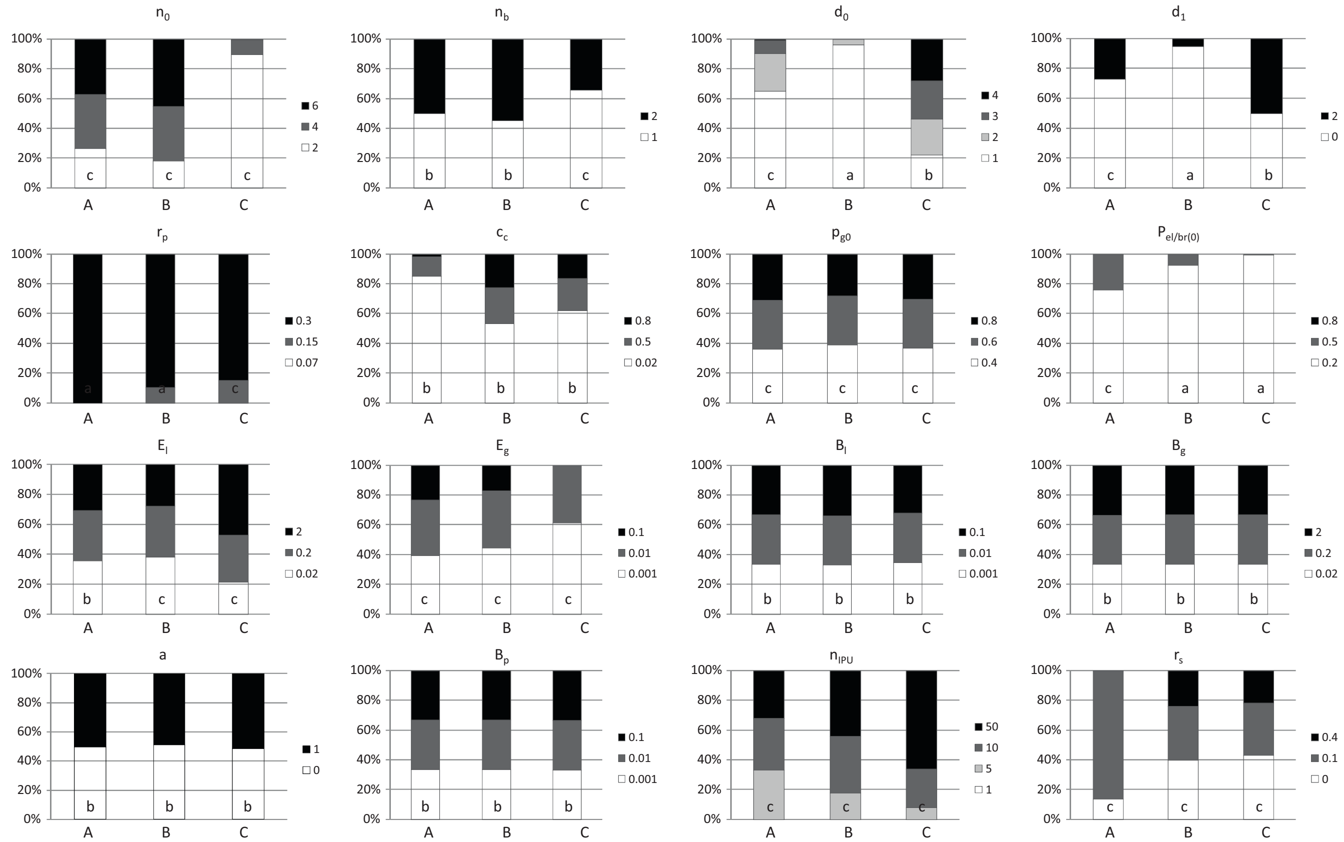


Fig. 3. Percentage of plants per value tested for each input parameter for the three performance criteria considered (and the respective matrix corresponding to the top 1% of best performances). (A) Plant total resources, (B) number of ramets, (C): maximum length of one branch. (a) Unique-value parameter, (b) equi-distributed parameter and (c): complex-distributed parameter. See Table 2 for symbols significance of input parameters.

Table 3
Pearson correlation coefficients between output performance parameters (*A*: plant total resources, *B*: number of ramets, *C*: maximum length of one branch). They were calculated on the three matrices [*A*], [*B*] and [*C*] corresponding to the top 1% of the best performance of *A*, *B* and *C*.

Variable 1	Variable 2	Top-performance *A*	Top-performance *B*	Top-performance *C*
A	*B*	0.43	0.29	0.58
A	*C*	−0.01	0.15	0.17
B	*C*	0.05	0.22	0.03

3. Results

3.1. Key processes interacting with plant performance

On matrixes [*A*], [*B*] and [*C*], we detected a low correlation between the plant total resources (*A*) and the maximum length of one branch (*C*) and between the number of ramets (*B*) and *C*. *A* and *B* were strongly correlated for top-performances *A* and *C* and less for top-performance *B* (Table 3).

On matrixes [*A*], [*B*] and [*C*], we recorded the three types of input parameters mentioned in Section 2.7 depending on plant distribution among the values tested for the parameter: unique value parameters, equi-distributed parameters and complex-distributed parameters (Fig. 3):

(1) *Unique value parameters*: For [*A*] (1 parameter), all plants were characterized by a high r_p. For [*B*] (4 parameters), all plants should have a high r_p, favor elongation over branching (low $p_{\mathrm{el/br(o)}}$), display a short and unvariable spacer length (low d_0 and d_1). For [*C*] (1 parameter), plants should favor elongation over branching.
(2) *Equi-distributed parameters*: This corresponded to 7, 6 and 7 parameters for [*A*], [*B*] and [*C*] respectively. For [*A*], [*B*] and [*C*], B_l, B_g, a and B_p had no influence on plant performance. We recorded as equi-distributed parameters: the maximum number of branches developing from ramets along branches n_b for [*A*] and [*B*], E_l for [*B*] and d_0 and d_1 for [C].
(3) *Complex-distributed parameters*: This category of profile was recorded for 8, 6 and 8 parameters out of 16 for [*A*], [*B*] and [*C*], respectively. Plant performance was high when r_p was high, c_c and $p_{\mathrm{el/br(o)}}$ were low and n_IPU higher than 1.

3.2. Plant strategies under optimal conditions of growth

Plants were grouped in three main clusters for the clustering analyses performed on [*A*] (8 input parameters) and [*C*] (8 input parameters). Four clusters were detected for [*B*] (6 input parameters). For clustering analyses performed on [*A*], [*B*] and [*C*], the clusters corresponded to groups of plants with similar mean performances in *A*, *B* and *C*, respectively (Table 4). These groups corresponded to different combinations of input parameters values. For [*A*], the three clusters differed mainly depending on the number of branches from the initial ramet (n_0) and the dependence of the elongation on the generation number (E_g) (Fig. 4a). For [*B*], the four clusters differed mainly depending on the number of branches from the initial ramet (n_0) and the dependence of the elongation process on the branch length and generation number (E_l and E_g) (Fig. 4b). For [*C*], the three clusters differed mainly depending on n_b, E_l, n_IPU and r_s (Fig. 4c).

4. Discussion

4.1. Limitations of the model

We made different biological assumptions which may limit the applicability of our results. As many other modeling studies, we focused on plants producing network structures. This restriction narrows the range of plants able to propagate via clonality as 17 clonal growth organs were detected in plants and some species are able to display several of them (Klimeš et al., 1997; Klimešovà and Klimeš, 2008; Klimešovà and de Bello, 2009).

Table 4
Clustering analysis using complex-distributed parameters for top 1% performance using criteria *A*, *B* and *C* (8, 6, 8 input parameters, respectively). 3, 4 and 3 clusters were detected for criteria *A*, *B* and *C*, respectively. Number of plants, mean and standard deviation (SD) of the performance criteria for each cluster.

	Mean ± SD	Number of plants
Top 1% performance (criteria A)		
Cluster 1	740.4 (173.3)	53,087
Cluster 2	761.5 (202.6)	63,733
Cluster 3	735.9 (180.0)	110,230
Top 1% performance (criteria B)		
Cluster 1	22.3 (2.8)	91,299
Cluster 2	22.8 (3.2)	71,984
Cluster 3	22.3 (2.5)	29,099
Cluster 4	22.2 (2.9)	34,776
Top 1% performance (criteria C)		
Cluster 1	19.6 (2.0)	80,730
Cluster 2	19.9 (2.3)	76,378
Cluster 3	20.4 (2.3)	69,859

While considering network structures, we considered a dichotomic metabolic role of ramet vs. connection organs into resource uptake vs. storage respectively. This simplification may be uncorrect for some species, especially plants with photosynthetic stolons (e.g. *Trifoliumrepens*) where photosynthetic activity may be up to 20% (on a unit area basis) of that in the leaves of ramets (Chapman and Robson, 1992). In these species, the production of resources by connections should increase the ecological benefits of developing connections (high metabolic gain through resource production and low cost) rather than ramets. On the contrary, ramets may have a role in resource storage by resource accumulation in the roots and the shoot basis (van der Meijden et al., 1988; Klimeš and Klimešová, 2002). In some species, storage is mainly confined at the ramet scale and connections only play a role in nutrient translocation (Kavanová and Gloser, 2005). A more profound work is therefore needed to adequately detail translocation/storage role of connections and its effect on plant performance.

Though including random variation in some traits, our model did not include the ability of plants to adjust plastically along the developmental stages. Most plant species are plastic at least for some of the studied traits such as elongation vs. branching or the level of physiological integration between ramets. These plastic adjustments may improve the foraging capacity of plants, promoting ramet placement in favorable sites and the escape of unfavorable sites (López et al., 1994). In the absence of interaction of plant growth with disturbance or resource spatial distribution, such plasticity should have been implemented in response to intraclonal competition. Modeling plant plastic response to competition needs to evaluate competitive pressure in the neighborhood of the new potential growth unit (through the density of surrounding ramets, Herben and Suzuki, 2001 or the calculation of competitive potential depending on the resource of the ramet, Oborny et al., 2000; Mágori et al., 2003). The effect of competitors on the focal growth unit should be also simulated as either a reduction of fecundity or biomass (Winkler and Klotz, 1997; Turnbull et al., 2004) or a change in the direction or length of the branch (Winkler and Klotz, 1997). Plant plastic responses to ramet density may have diminished intraclonal competition and had a significant effect on the output parameters.

4.2. Performance traits of clonal individuals

Top-individuals reached performances that could be compared to real plants though the purpose of the present study was not

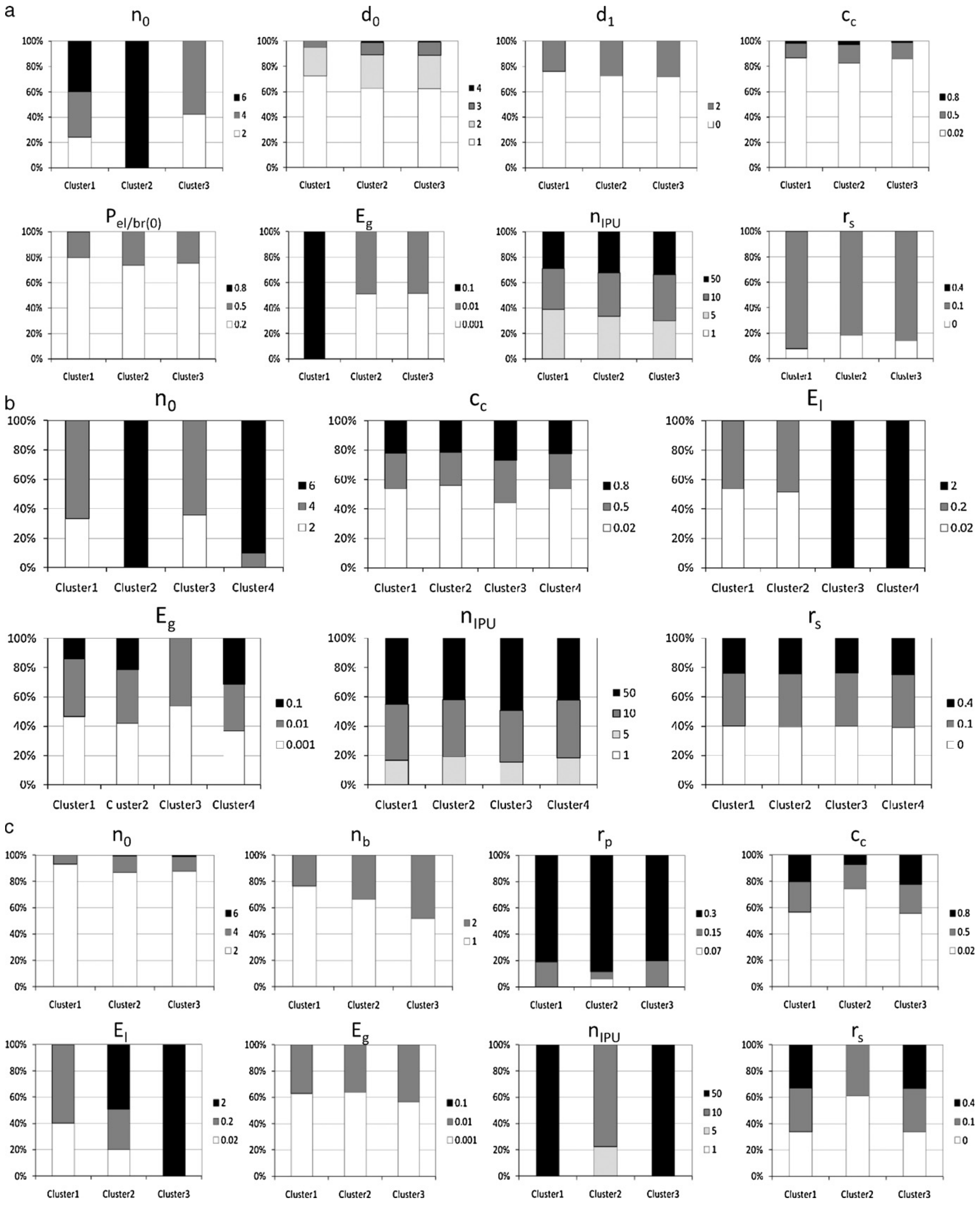


Fig. 4. Percentage of plants per value tested per cluster for each input parameter. (a) Clustering analysis using the 8 complex-distributed parameters detected for top-performance A; (b) clustering analysis using the 6 complex-distributed parameters detected for top-performance B; (c) clustering analysis using the 8 complex-distributed parameters detected for top-performance C. See Table 2 for abbreviations of input parameters.

to precisely calibrate the model on real plants as was found for instance in Winkler and Klotz (1997) or Wildovà et al. (2007). Plant total resource used in the model may have the meaning of plant biomass though it is difficult to precisely compare the resource amount used in the model to biomass measures in plants. The number of ramets and the maximum length of a branch were however comparable to the experimental data collected on 10 meadow species in our controlled experiment (Benot et al., 2009). The ramet number produced from one transplanted ramet varied after one season from 5 for *Carexdivisa* or *Juncusgerardi* to more than 85 for *Agrostisstolonifera* with most of the studied species in the range of 10–40 ramets. The maximum length of a connection reached 4–41 cm for rhizomateous species and 40–109.9 cm for stoloniferous species (Benot et al., 2009). These experimental data may be comparable with our virtual results if we consider that a ramet unit (i.e. a growth unit) takes about 2 cm × 2 cm. Further comparison of these results to data collected in field studies should however be proceeded carefully as no interspecific competition, stress or disturbance were implemented in the model.

The number of ramets was correlated as expected with plant total resources. This correlation was however low for one out of the three optimizations. The absence of correlation between the maximum length of one branch and plant resources is surprising. Genet size has indeed been reported to influence the structure of the rhizome network of *Solidagoaltissima* (Meyer and Schmid, 1999). Correlation coefficients depended strongly on the performance output optimized, either in the degree or in the sign. Optimization of different performance measures may therefore probably be reached by different combinations of plant-trait values.

4.3. Key processes interacting with plant performance

At least one of the performance traits was the highest with: (i) a high metabolic gain (high r_p; low c_c), a low resource storage (r_s) and a high distance of integration (n_IPU); (ii) a dominant effect of elongation against ramification (low $p_{\mathrm{el/br}(0)}$) and of the position and number of meristems (n_0, d_0, d_1). However these processes were not similarly significant for all performance criteria.

Metabolic parameters were unsurprisingly particularly determining plant total resources and ramet production. This similarity was partly due to the high correlation between these two output parameters as explained earlier. Biomass production was maximized when photosynthesis was high and connection production uncostly. Low long-term resource storage and high integration were determinant for ramet production and space colonization (promoted by lengthy branches). Within the context of modeling, long-term storage may be non-adaptive as it represents an immediate cost for the plant by diverting resources that could support short-term growth (Chapin et al., 1990). Simulating a single season probably underestimates the utility of storage which should help supporting spring growth the year after (Price et al., 2002). Storage should also be crucial for the survival of newly formed ramets in unstable or disturbed environments (Stuefer and Huber, 1999; Suzuki and Stuefer, 1999) or the regrowth of damaged ramets (Turner and Pollock, 1998). These aspects should be implemented in a further version of the model.

In two out of the three performance traits (ramet production and space colonization), we recorded a dominant effect of elongation against ramification for increasing plant performance. Elongation minimizes the overlap between feeding sites and hence intra-genet competition (Bell, 1984). Intragenet competition modeled in the present study as a simple rule on space occupation by ramets gives indeed a particular advantage to guerrilla species where elongation predominates over branching. These species are particularly efficient at exploring the environment under non-limiting conditions of growth (Kleijn and van Groenendael, 1999) whereas phalanx species characterized by highly branched and dense systems should be promoted in competitive environments (Schmid and Harper, 1985; Humphrey and Pyke, 1998).

Spatial occupation was promoted by a low number of meristems on the initial ramet, whereas the number of meristems at each branch node had no effect. Two meristems with long branches may enable the exploration of space at greater distances from the initial ramet and therefore promote long-distance ramet dispersal, whereas a clumped architecture should tend to prevent the intrusion of other plants in its occupied area (Smith and Palmer, 1976; Gough et al., 2002; Brun et al., 2007). The number and position of meristems are therefore more determinant in clonal plant performance than the spatial positioning of branches (determined through B_l, B_g, B_p) which seemed to have little influence. Spatial positioning of branches may depend also on the angles of branching which have not been taken into account in the present grid-model. Other continuous models of clonal plant growth have demonstrated however that angles between branches may govern spatial exploration and intragenet competition (Smith and Palmer, 1976; Bell, 1979). These theoretical demonstrations were not confirmed however in the calibrated-model of Wildovà et al. (2007).

Spacer length was recorded as a key parameter for determining ramet production in contrast to space colonization. The increase in the number of ramets with the decrease of the spacer length and the absence of variability of it may be related to the modeling assumptions and update process where (1) the position of ramet is determined by local spacer length, (2) spacer lengths were calculated at the start of the simulation rather than at each time step. The choice of local spacer length was therefore independent of the position of existing ramets and did not result from a plastic adjustment of growth in response to the local density of ramets. Plastic adjustment of spacer length in response to competition was demonstrated in experimental works, though no clear consensus was found between the different surveys: in some species, spacer length increases in response to competitive pressure (Weijschedé et al., 2008) whereas in some others it decreases (Cheplick and Gutierrez, 2000; Marcuvitz and Turkington, 2000). In a simulation study, Herben and Suzuki (2001) have demonstrated that higher spacer length may decrease intra-genet competition but Schmid (1986) underlined that it could be beneficial for plants to either shorten or lengthen their stolons, depending on the relative impact of intra and inter-clonal contacts.

For most input parameters, a complex distribution of the number of simulations within the values tested was detected. These results therefore suggest interactive effects between the input parameters.

4.4. Toward different plant strategies for the same performance under optimal growth conditions?

Clustering analyses highlighted different combinations of traits promoting similar performance. These combinations differed by small variations in the distribution of parameter values between clusters. This result is strongly innovative. Earlier modeling studies demonstrated that there is not a single, general solution for plant optimal foraging in plants but that one strategy may be selectively advantageous under a certain, often narrow, range of environments (Oborny, 1994). We demonstrated further that even under the same growth environment, different strategies may promote similar plant performance. Some other modeling studies evaluate the impact of input parameter on plant performance by testing one parameter at a time and fixing the others. If this process has the benefit to restrict the number of simulations and the calculation power needed, it assumes that input parameters may have independent effects. The exhaustive browsing of the whole parameter space demonstrated here that for most parameters, this assumption is invalidated. The non-additive effect of input parameters was suggested in the modeling study of Herben and Suzuki (2001), which chose the alternative to calibrate the input parameters on real plants.

In theory, slightly different combinations of clonal traits may therefore be selected in the same growth environment. In real situations, the dominance of one particular strategy or the coexistence of several strategies may be determined by local filters such as competitive pressure, disturbance or nutrient availability which were not taken into account in the present study. The highly modular implementation of this model should allow easily in further versions to simulate the interactions of several clones (i.e. a population) and their dynamics while coupled non-linearly with a model simulating the ground flow of nutrients (Garbey et al., 2008).

4.5. The interest of volunteer computing for studying ecological processes

New quality of insight into ecological processes can be obtained by the computational approach presented here. At this point, the Virtual Prairie project counts around 2500 users with more than 9000 attached computers and is therefore a medium size project compared to the much older projects like SETI@HOME or Climate Prediction. Although only 1/3 of these resources were available to the project at a given time, it represented much more computing power and at a very cheap cost than any local resource we could have got. Compared to single-computer simulations, volunteer computing enhanced the computing capacity and enabled to study the effect of a large number of traits simultaneously. Associated with systematic data-mining of the results, this approach may give enough information on the parameter landscape to localize potential interesting patterns, detect emerging properties that were not anticipated or draw the limits of the model. It necessitates however non-trivial data analysis for large datasets. The next step will consist to refine the analysis with multiple criteria optimization with stochastic parallel algorithms similar to Smaoui-Feki et al. (2009). The use of volunteer computing should have also an obvious social aspect as it brings to the attention of the general public scientific questions in ecology.

Acknowledgements

The authors wish to thank David Anderson from the Berkeley Space lab for his advise with BOINC, and Keith Crabb, manager of the research computing center and the IT – high performance computing Group at University of Houston for his invaluable help with the ViP project. We thank also the 2200 volunteers worldwide that contributed to the calculations. We thank also P. Hulmes for English corrections. This project benefited from the grant ANR-08-SYSC-012 of the Agence Nationale de la Recherche.

References

Alpert, P., 1996. Nutrient sharing in natural clonal fragments of Fragariachiloensis. J. Ecol. 84, 395–406.

Anderson, D.P., 2004. BOINC: A System for Public-Resource Computing and Storage. In: Proceedings of the 5th IEEE/ACM International Workshop on Grid Computing, Pittsburgh, USA, pp. 1–7.

Anderson, D.P., Cobb, J., Korpela, E., Lebofsky, M., Werthimer, D., 2002. SETI@home: an experiment in public-resource computing. Assoc. Comput. Mach. 45, 56–61.

Asaeda, T., Rajapakse, L., Manatunge, J., Sahara, N., 2006. The effect of summer harvesting of Phragmites australis on growth characteristics and rhizome resource storage. Hydrobiology 553, 327–335.

Bell, A.D., 1979. The hexagonal branching pattern of rhizomes of Alpiniaspeciosa L.(Zingiberaceae). Ann. Bot. 43, 09–223.

Bell, A.D., 1984. Dynamic morphology: a contribution to plant population ecology. In: Dirzo, R., Sarukhan, J. (Eds.), Perspectives in Plant Population Ecology. Sinauer, Sunderland, pp. 48–65.

Benot, M.L., Mony, C., Puijalon, S., Esmaeili, M.M., Van Alphen, J.J.M., Bouzille, J.B., Bonis, A., 2009. Responses of clonal architecture to experimental defoliation: a comparative study between ten grassland species. Plant Ecol. 201, 621–630.

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

Birch, C.P.D., Oom, S.P., Beecham, J.A., 2007. Rectangular and hexagonal grids used for observation, experiment and simulation in ecology. Ecol. Model. 206, 347–359.

Brun, F., Cummaudo, F., Olivé, I., Vergara, J., Pérez-Lloréns, J., 2007. Clonal extent, apical dominance and network in features in the phalanx angiosperm Zostera-noltiiHornem. Marine Biol. 151, 1917–1927.

Chapin III, F.S., Schulze, E.D., Mooney, H.A., 1990. The ecology and economics of storage inplants. Ann. Rev. Ecol. Syst. 21, 423–447.

Chapman, D.F., Robson, M.J., 1992. The physiological role of old stolonmaterial in white clover (Trifoliumrepens L.). New Phytol. 122, 53–62.

Cheplick, G.P., Gutierrez, C.M., 2000. Clonal growth and storage in relation to competition in genets of the rhizomatous perennial Amphibromus scabrivalvis. Can. J. Bot. 78, 536–546.

D'Hertefeldt, T., Jónsdóttir, I.S., 1999. Extensive physiological integration in intact clonalsystems of Carexarenaria. J. Ecol. 87, 258–264.

de Kroon, H., Hutchings, M.J., 1995. Morphological plasticity in clonal plants: the for aging concept reconsidered. J. Ecol. 83, 143–152.

Fagerström, T., 1992. The meristem–meristem cycle as a basis for defining fitness in *clonal* plants. Oikos 63, 449–453.

Garbey, M., Mony, C., Smaoui, M., 2008. Parallel Multiscale Software for fluid flow – Agent Based Hybrid Models. In: Proceedings of the 20th international Conference of Parallel Computational Fluid Dynamics, 18–22 May 2008, France.

Gardner, S.N., Mangel, M., 1999. Modeling investments in seeds, clonal offspring, and translocation in a clonal plant. Ecology 80, 1202–1220.

Gough, L., Goldberg, D.E., Hershock, C., Pauliukonis, N., Petru, M., 2002. Investigating the community consequences of competition among clonal plants. Evol. Ecol. 15, 547–563.

Hartnett, D.C., 1989. Density- and growth stage-dependent responses to defoliation in two rhizomatous grasses. Oecologia 80, 414–420.

Herben, T., Hara, T., 1997. Competition and spatial dynamics of clonal plants. In: de Kroon, H., van Groenendael, J. (Eds.), The Ecology and Evolution of Clonal Plants. Backhuys Publishers, Leiden, pp. 331–358.

Herben, T., Suzuki, J., 2001. A simulation study of the effects of architectural constraints and resource translocation on population structure and competition in clonal plants. Evol. Ecol. 15, 403–423.

Huber, H., Stuefer, J., 1997. Shade-induced changes in the branching pattern of a stoloniferousherb: functional response or allometric effect? Oecologia 110, 478–486.

Humphrey, L.D., Pyke, D.A., 1998. Demographic and growth responses of a guerilla and a phalanx perennial grass in competitive mixtures. J. Ecol. 86, 854–865.

Hutchings, M.J., Bradbury, L.K., 1986. Ecological perspectives on clonal perennial herbs. BioScience 36, 178–182.

Hutchings, M.J., Mogie, M., 1990. The spatial structure of clonal plants: control and consequences. In: de Kroon, H., van Groenendael, J. (Eds.), Clonal Growth in Plants: Regulation and Function. SPB Academic Publishing, The Hague, The Netherlands, pp. 57–78.

Jónsdóttir, I.S., Watson, M.A., 1997. Extensive physiological integration: an adaptive trait in resource limited environments? In: de Kroon, H., van Groenendael, J. (Eds.), The Ecology and Evolution of Clonal Growth in Plants. Backhuys Publishers, Leiden, pp. 109–136.

Kavanová, M., Gloser, V., 2005. The use of internal nitrogen stores in the rhizomatous grass Calamagrostis epigejos during regrowth after defoliation. Ann. Bot. 95, 457–463.

Kelly, C.K., 1995. Thoughts on clonal integration: facing the evolutionary context. Evol. Ecol. 9, 575–585.

Kleijn, D., van Groenendael, J.M., 1999. The exploitation of heterogeneity by a clonal plant in habitats with contrasting productivity levels. J. Ecol. 87, 873–884.

Klimeš, L., Klimešová, J., Hendricks, R., van Groenendael, J., 1997. Clonal plant architecture: a comparative analysis of form and function. In: de Kroon, H., van Groenendael, J. (Eds.), The Ecology and Evolution of Clonal Plants. Backhuys Publishers, Leiden, The Netherlands, pp. 1–29.

Klimeš, L., Klimešová, J., 2002. The effects of mowing and fertilization on carbohydrate reserves and regrowth of grasses: do they promote plant coexistence in species-rich meadows? Evol. Ecol. 15, 363–382.

Klimešovà, J., Klimeš, L., 2008. Clonal growth diversity and bud banks of plants in the Czech flora: an evaluation using the CLO-PLA3 database. Preslia 80, 255–275.

Klimešovà, J., de Bello, F., 2009. CLO-PLA: the database of clonal and bud bank traits of Central European flora. J. Veg. Sci. 20, 511–516.

Kun, Á., Oborny, B., 2003. Survival and competition of clonal plant populations in spatially and temporally heterogeneous habitats. Com. Ecol. 4, 1–20.

Landa, K., Benner, B., Watson, M.A., Gartner, J., 1992. Physiological integration for carbon inmayapple (Podophyllum peltatum), a clonal perennial herb. Oikos 63, 348–356.

Liao, M., Yu, F., Song, M., Zhang, S., Zhang, J., Dong, M., 2003. Plasticity in R/S ratio, morphology and fitness-related traits in response to reciprocal patchiness of light and nutrients in the stoloniferous herb, Glechoma longituba L. Acta Oecol. 24, 231–239.

López, F., Serrano, J.M., Acosta, F.J., 1994. Parallels between the foraging strategies of ants and plants. TREE 9, 150–153.

MacQueen, B., 1967. Some Methods for classification and Analysis of Multivariate Observations. In: Proceedings of 5-th Berkeley Symposium on Mathematical Statistics and Probability, Berkeley, USA, pp. 281–297.

Mágori, K., Oborny, B., Dieckmann, U., Meszena, G., 2003. Cooperation and competition in heterogeneous environments: the evolution of resource sharing in clonal plants. Evol. Ecol. Res. 5, 787–817.

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

Marshall, C., 1990. Source-sink relations of interconnected ramets. In: van Groenendael, J., deKroon, H. (Eds.), Clonal Growth in Plants: Regulation and Function. SPB Academic Publishing, The Hague, pp. 23–41.

McLellan, A.J., Prati, D., Kaltz, O., Schmid, B., 1997. Structure and analysis of phenotypic andgenetic variation in clonal plants. In: de Kroon, H., van Groenendael, J. (Eds.), The Ecology and Evolution of Clonal Plants. Backhuys Publishers, Leiden, pp. 185–210.

Meyer, A., Schmid, B., 1999. Experimental demography of rhizome populations of establishing clones of Solidago altissima. J. Ecol. 87, 42–54.

Oborny, B., 1994. Growth rules in clonal plants and environmental predictability—a simulation study. J. Ecol. 82, 341–351.

Oborny, B., Cain, M., 1997. Models of spatial spread and foraging in clonal plant species. In: de Kroon, H., Van Groenendael, J. (Eds.), The Ecology and Evolution of Clonal Plants. Blackhuys Publications, Leiden, The Netherlands, pp. 155–184.

Oborny, B., Kun, A., Czárán, T., Bokros, S., 2000. The effect of clonal integration on plant competition for mosaic habitat space. Ecology 81, 3291–3304.

Price, E.A.C., Marshall, C., Hutchings, M.J., 1992. Studies of growth in the clonal herb Glechoma hederacea. I. Patterns of physiological integration. J. Ecol. 80, 25–38.

Price, E.A.C., Hutchings, M.J., 1992. The causes and developmental effects of integration and independence between different parts of Glechoma hederacea clones. Oikos 63, 376–386.

Price, E.A.C., Gamble, R., Williams, G.G., Marshall, C., 2002. Seasonal patterns of partitioning and remobilization of 14C in the invasive rhizomatous perennial Japanese knotweed (Fallopia japonica (Houtt.) RonseDecraene). Evol. Ecol. 15, 347–362.

Puijalon, S., Bornette, G., Sagnes, P., 2005. Adaptations to increasing hydraulic stress: morphology, hydrodynamics and fitness of two higher aquatic plant species. J. Exp. Bot. 56, 777–786.

Rousseeuw, P.J., 1987. Silhouettes: a graphical aid to the interpretation and validation of cluster analysis. J. Comput. Appl. Math. 20, 53–65.

Sackville-Hamilton, N.R., Schmid, B., Harper, J.L., 1987. Life-history concepts and the population biology of clonal organisms. Proc. Royal Soc. London 232, 35–57.

Schmid, B., 1986. Spatial dynamics and integration within clones of grassland perennials with different growth form. Proc. Royal Soc. London 228, 173–186.

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

Sintes, T., Marba, N., Duarte, C., Kendrick, G., 2005. Nonlinear processes in seagrass colonisation explained by simple clonal growth rules. Oikos 108, 165–175.

Smaoui-Feki, M., Nguyen, V.H., Garbey, M., 2009. Parallel Genetic Algorithm Implementation for BOINC. In: Proceedings of the International Conference on Parallel Computing, 1–4 September 2009, Lyon, France.

Smith, A.P., Palmer, J.O., 1976. Vegetative reproduction and close packing in a successional plant species. Nature 261, 232–233.

Steen, E., Larsson, K., 1986. Carbohydrates in roots and rhizomes of perennial grasses. New Phytol. 104, 339–346.

Stöcklin, J., Winkler, E., 2004. Optimum reproduction and dispersal strategies of a clonal plant in a metapopulation: a simulation study with Hieracium pilosella. Evol. Ecol. 18, 563–584.

Stuefer, J.F., Huber, H., 1999. The role of stolon internodes for ramet survival after clone fragmentation in Potentilla anserina. Ecol. Lett. 2, 135–139.

Sutherland, W.J., Stillman, R.A., 1990. Clonal growth: insights from models. In: van Groenendael, J., de Kroon, H. (Eds.), Clonal Growth in Plants: Regulation and Function. SPB Academic Publishing, The Hague, The Netherlands, pp. 95–112.

Suzuki, J.I., Stuefer, J.F., 1999. On the ecological and evolutionary significance of resource storage in clonal plants. Plant Species Biol. 14, 11–17.

Turner, L.B., Pollock, C.J., 1998. Changes in stolon carbohydrates during the winter in four varieties of white clover (Trifolium,repens L.) with contrasting frost hardiness. Ann. Bot. 81, 97–107.

Turnbull, L.A., Coomes, D., Hector, A., Rees, M., 2004. Seed mass andthe competition/colonization trade-off: competitive interactions and spatial patterns in a guild of annual plants. J. Ecol. 92, 97–109.

van der Meijden, E., Wijn, M., Verkaar, H., 1988. Defence and regrowth, alternative plant strategies in the struggle against herbivores. Oikos 51, 355–363.

Watson, M.A., 1986. Integrated physiological units in plants. TREE 1, 119–123.

Weijschedé, J., Berentsen, R., de Kroon, H., Huber, H., 2008. Variation in petiole and internode length affects plant performance in *Trifoliumrepens* under opposing selection regimes. Evol. Ecol. 22, 383–397.

Wikberg, S., 1995. Fitness in clonal plants. Oikos 72, 293–297.

Wildovà, R., Gough, L., Herben, T., Hershock, C., Goldberg, D., 2007. Architectural and growth traits differ in effects on performance of clonal plants: an analysis using a field-parameterized simulation model. Oikos 116, 836–852.

Winkler, E., Fischer, M., 1999. Two fitness measures for clonal plants and the importance of spatial aspects. Plant Ecol. 141, 191–199.

Winkler, E., Klotz, S., 1997. Clonal plant species in dry-grassland community: a simulation study of long-term population dynamics. Ecol. Model. 96, 125–141.