Rhizome: a model of clonal growth

(version September 2001)

Basic features

The model is able to capture the following processes:

- horizontal growth, branching and fragmentation of horizontal structures (e.g. rhizomes) bearing ramets;
- formation of primary (long, unbranched, fast growing, no ramets attached) and secondary (short, more branched, with ramets attached) rhizomes
- ramet formation at any position at the rhizome
- effects of intraspecific and interspecific neighbourhood competition on horizontal growth, branching and ramet formation and mortality; different shapes of competitive asymmetry can be handled
- Resource (photosynthate) translocation within rhizomes
- different sizes of ramets and rhizomes
- nonzero radius and shape change of ramets
- density independent mortality of ramets, and mortality due to limited lifespan
- each species may have different plastochron time
- establishment from seed and tracking genetic origin of all the rhizomes and ramets
- juvenile stage of variable duration with ‘unitary’ growth type.
- density-independent mortality due to disturbance (such as fire)

Basic processes in the model

Model objects

The model works with 4 classes of objects: (i) nonclonal plants (come into being by seed establishment, do not change position, but grow in size), (ii) rhizomes/rhizome fragments (come into being from non-clonal plants or by fragmentation of larger rhizome systems), (iii) nodes (these are the units that compose rhizomes), and (iv) ramets (photosynthetically active plant parts that provide resource for rhizome growth; they may be attached either to non-clonal plants or to nodes).

The following variables are defined for each non-clonal plant:

- genetic identity (genotype code)
- species code
- time of establishment from seed (non-clonal plant age)
- (ramet is present by default in non-clonal plants: death of the ramet means death of the whole plant)

The following variables are defined for each rhizome fragment:

- genetic identity (genotype code)
- species code

- time of establishment from seed
- list of all nodes and ramets attached

After the clonal growth begins, plants form rhizomes composed of nodes. The following variables are defined for each node of a rhizome system:

- Topological variables: link to the younger node, older node, branch, link to the rhizome
- coordinates in space
- resource for further lateral growth
- second size dimension - e.g. vertical position, or area occupied
- whether it bears a ramet or not
- presence of the active meristem (for terminal nodes only)

The following variables are defined for each ramet:

- coordinates in space – link to the appropriate node if on a clonal fragment, or to the non-clonal plant
- ramet size
- time step when a ramet was born (ramet age)

Modelled processes (more detailed description of most of the processes in the following section)

It simulates growth of clonal plants on a plane with toroidal boundaries. It works with several (currently up to 5) species; each of these species is allowed to have a different set of growth and architectural parameters.

A typical model run begins with establishment of propagules in the plane. Each propagule has a distinct genetic identity and belongs to a species (this defines its set of species-specific parameters used for its simulation). Through the whole simulation, the species and genetic identity of non-clonal plants and rhizome fragments that arose from them is maintained. These propagules give rise to nonclonal plants; these nonclonal plants change into clonal plants, which grow horizontally, branch, produce ramets and interact.

The following **propagule establishment** processes are modelled:

- number of plants establishing at the beginning (ISR regime)
- number of plants establishing at each time step (RSR regime); both regimes can be combined
- (These propagules give rise to plants that grow non-clonally or clonally, depending on parameters)

The following processes are modelled for each **non-clonal plant**:

- ramet growth processes (of the ramet forming the non-clonal plant). These ramet processes are identical to the processes of ramets of clonal plants, but use different set of constants.
- decision whether the nonclonal plant will give rise to a clonal plant (i.e. change into rhizome fragments). The criterion is based either on resource or on time steps), they begin clonal growth. If they begin the clonal growth, they may form one or more (initially connected) rhizome fragments.

The **rhizome** grows/changes by the following processes (*this section combines processes taking place at the level of rhizomes and at the level of nodes; specification is added in parentheses after each process*):

- adding a new node at the tip. The ramet from the previous node remains attached to the tip (this is means that the default for the 2nd youngest node is no ramet present; it could, however, be added by the lateral ramet formation). The length and angle of the internode are independent of the internal state of the rhizome and of its neighbourhood. Note that the terminal ramet is shifted always to the youngest node. Before the adding a new node, translocation takes place to determine the amount of available resource. When a new node is added, it may be either a secondary (=ordinary) rhizome (one node long, internode length identical to the internode length of the main axis) or a primary rhizome, which is several nodes long and its internodes are of different length than internodes of the main axis. The primary rhizome is formed as a means to escape if the neighbouring ramet density is high and resource is still sufficient. (*process taking place at terminal nodes*)
- branching at the tip and formation of a new ramet at the end of the branch. This happens when the lateral bud is activated at the same time as the terminal bud. Branching angle is independent of the internal state of the rhizome and of its neighbourhood; left/right branching decision is made on the basis neighbourhood ramet density: the branch is made always in the direction of lower density. Before a branch formation, translocation takes place to determine the amount of available resource. (*process taking place at terminal nodes*)
- formation of lateral ramets. These ramets are formed when density of the neighbours is low and resource is sufficient (*process taking place at all nodes*)
- activation of sleeping buds to form new branches. They are formed when resource is sufficient (*process taking place at all nodes*)
- nodes at the oldest part die. It dies after a specified number of time steps (this produces rhizomes of the same length, though this length may be species-specific). If a branching node occurs at the basipetal position, the rhizome is split into two (while their species and genetic identity is maintained). (*process taking place at basipetal nodes*)
- The terminal bud may die; in this case the rhizome stops growing (but there still may be some ramets on it). (*process taking place at terminal nodes*)

The following processes are modelled for each **ramet** (both on a non-clonal plant and on a clonal plant):

- growth in size
- resource production/accumulation
- mortality (based on the resource criterion or on age criterion)

Specific structural assumptions in the model

Ramet growth in size

Ramet sizes are expressed in units (with the meaning of mass) determined by the values of parameters x_{init} and K_{c}. The ratio of these two parameters determines the size variation of the plant; if $x_{\text{init}} = K_{\text{c}}$, all the ramets are of identical sizes. Otherwise ratio of these parameters means the maximum ramet size that the species can attain relative to the initial ramet size (ramet size formed after seedling establishment). If only one species is simulated, only one of these two values is a true parameter (the other one determines the scale only); if there are more species, both are needed since relative ramet sizes have to be defined among species. It should be kept in mind that scale used for these parameters affects other parameters that are expressed using biomass units.

The ramet growth follows the formula:

$$x_{t+1} = \max\, [x_t + r_{\text{c}} \,.\, R_t \,.\, (1 - f_{\text{c}}) \,.\, (K_{\text{c}} - x_t) / (1 + \alpha \,.\, (1 - f_{\text{c}}) \,.\, R_t),\, x_{\text{init}}\,] \quad (1)$$

where x_t is the ramet size at the time t, r_{c} is the growth rate for that species, K_{c} is the maximum ramet size for that species, α is the resource-dependence constant for that species (mediates density-dependence), f_{c} is the fraction of resource stored and not used for the size growth and R_t is the resource available at the node supporting the ramet. Units of the constants are: K [g], r [t^{-1}], α [1/resource]. If α is very small relative to K_{c} and r_{c}, growth of the ramet will be linearly dependent on the product of resource available and difference of actual and maximum size. This is likely to produce diverging behaviour of the ramet size instead of convergence towards the value of K_{c}. There is a test done that flags runs in which divergence takes place (i.e. the size of a ramet calculated using the first argument of the **max** function above is smaller than x_{init}), and some care is needed in interpretation of their results. (NB. The **max** function in the equation above is a safeguard against negative ramets sizes in case of such a diverging behaviour.) The same formula (with different constants for nonclonals) is used for terminal ramets, lateral ramets and non-clonal plants. Time is expressed in plastochrons for rhizomes and in time steps in non-clonal plants.

Resource is consumed by the growth in size. This is determined by the value of f_{c}. All resource used for the size growth is consumed.

Resource production/accumulation

Resource is expressed in arbitrary units (with the meaning of mass or energy). The scale of these units is given by the fact that the resource of a plant establishing from seed (R_{init}) is arbitrarily set to 1. Constants of resource levels (not multiplicative constants, such as S below) thus have the meaning of 'resource relative to the resource of a plant establishing from seed'.

In all nodes the resource is accumulated following this formula:

$$R_{t+1} = S \,.\, R_t \,.\, f_{\text{c}} + A \,.\, (x_t / x_{\text{init}}) \,.\, (1 - \beta \,.\, N) / (1 + \beta \,.\, N), \qquad (2)$$

where R_t is the resource of the ramet at the time t, x_t is the ramet size at the time t (when $\beta \,.\, N < 1$) and x_{init} otherwise, S is the proportion of the resource retained at the node (1 – respiration), f_{c} is the fraction of resource not used for the size growth (only for nodes bearing ramets; for nodes not bearing ramets $f_{\text{c}} = 1$), A is the accumulation rate, β is the density-dependence constant of resource accumulation for that species and N is the neighbourhood effect (see Eq. (3)).

Units of the constants are: R [resource], S [1], β [m^2], A [1]. Comments on the constants:

(i) The 'resource retained' S expresses how much of the resource from the earlier step is retained into the current step; if it equal 0, no resource is retained; it it equals 1, no resource is lost (except that used to produce ramets or branches) over time.

(ii) Density dependence in resource accumulation β: this is introduced to account for the fact that if neighbour density is very high, the photosynthetic balance will be negative and the net resource has to decrease. Note that if β equals zero, there is no density dependence in resource accumulation (it is simply proportional to ramet size). The resource produced will be zero when $N = 1/\beta$; if N is greater than $1/\beta$, the resource will decrease (or be negative if $S = 0$). Again, only neighbouring ramets are considered; presence of rhizomes has no effect on growth, resource accumulation and competition. NB. Meaning and numerical value of β is affected by the exact form used to define neighbourhood effect (3a or 3b).

(iii) The accumulation rate A expresses amount of resource produced in one time step per unit ramet size. Its value after subtraction of 1 means how many new ramets a ramet would be able to form per one plastochron under no-competition conditions. It is a non-dimensional constant. More on this constant in the 'Temporal variability' section.

The neighbourhood effect may have two different forms:

(1) for ramets of zero radius (if *diam_a* == 0 for all species) it is the following quantity:

$$N = \sum_{d(i) < D} (x_i / x)^{\theta} \qquad (3a),$$

where x_i is the size of the neighbouring ramet i, x is the size of the focal ramet (x_t for the current case), d(i) is the Euclidean distance of the ramet i from the focal ramet, D is the neighbourhood size and θ is the constant of competitive asymmetry (0 means perfect symmetry, 1 means perfect size-symmetry and >1 means size asymmetry; ∞ means complete one-sided asymmetry). Summation is done over all ramets that are within the circle with the focal ramet in its centre and radius of neighbourhood size. Different formulas are used for negative and positive resource change to account for the fact that production and respiration are different processes.

(2) for ramets of non-zero radius (if *diam_a* > 0 for all species) it is the following quantity:

$$N = \sum_{d(i) < D} O_i (x_i / x)^{\theta} \qquad (3a),$$

where O_i is the overlap of the zone of influence of the focal ramet and of the ramet i; meaning of the other parameters as above.

NB. The formulas 3a and 3b cannot be combined in a single simulation run. The program will not run if some species have ramets of non-zero radius and some other have ramets of zero radius.

NB. Competition involves only ramets (i.e. aboveground structures). Rhizomes and nodes do not 'see' each other.

Resource translocation

Translocation takes place at all nodes, no matter whether terminal or not, or whether they bear a ramet or not. Translocation is driven by the resource available at potential donor nodes. Each donor node searches for potential sinks up to the distance given by the parameter T (*sharing_range*), both basipetally and acropetally; all relevant branches in the acropetal direction are also scanned. Branches in the basipetal direction are not scanned, as thus would involve combination of basipetal (first) and acropetal (later) translocation. At each plastochron, each (donor) node j evaluates the following quantity:

$$U_j = \sum_{d(i,j)<T} D_i \,.\, B_i \qquad (4a),$$

where $d(i,j)$ is the distance of nodes i and j along the rhizome in acropetal or basipetal direction, measured in nodes, T is the translocation distance (identical both acropetally and basipetally), D_i is the weight determining the sink strength of the ith node (1 for non-terminal nodes bearing a ramet, *p_trans_tip* for terminal nodes bearing a ramet, and *p_trans_node* for non-terminal nodes not bearing a ramet) and B_i is the relative weight of basipetal vs. acropetal transport (*p_basipet* if the ith node is positioned basipetally relative to the donor node and 1 – *p_basipet* otherwise).

At the next stage, each (acceptor, i) node up to the distance T nodes from the donor node gets from the donor (j) node the following amount of resource

$$R_{\mathrm{added}}\,(i,j) = (1 - C_{\mathrm{T}})^{d(i,j)}\, D_i \,.\, B_i \;\; R_j \,.\, f_{\mathrm{tr}} \;/\; U_j \qquad (4b),$$

where R_j is the resource level of the donor ramet, f_{tr} is the proportion of the resource that is available for translocation, C_{T} is the cost of translocation (the resource fraction that is lost when translocated over one node) and T is the translocation distance (number of nodes over which translocation takes place). For each acceptor node, R_{added} is summed over all potential donor nodes; the resulting amount of resource is added to R_{avail}, i.e. the resource used to make decisions on growth and branching. Resource in each donor node involved in translocation has its resource diminished to $R_j\,.(1 - f_{\mathrm{tr}})$; the difference between this quantity and the quantity brought to the sink node is due to translocation cost. Each node of course serves both as acceptor and donor. As the result, R_{avail} is given by

$$R_{\mathrm{avail}}\,(i) = R_i \,.\, (1 - f_{\mathrm{tr}}) + \sum_{d(i,j)<T} R_{\mathrm{added}}\,(i, j) \qquad (4c)$$

If $U_j = 0$ (i.e. no acceptor nodes are within the translocation distance), no translocation takes place and all resource is kept at the donor node ($R_{\text{avail}}(i) = R_i$). Translocation takes place *always*, no matter whether the node involved happens to have sufficient resource for growth or branching or not.

NB. Note that for $T = 0$ or $f_{\text{tr}} = 0$, the model defaults to a usual architectural model without translocation.

Condition for growth: formation of the terminal ramet

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

$$R_{\text{avail}} > C_{\text{i}} + R_{\text{min}} / f_{\text{g}} \qquad (5)$$

where R_{avail} is the value defined by eq (4), C_{i} is the internode cost, f_{g} is the proportion of resource put into the new ramet at the growing tip, R_{min} is the minimum resource required for ramet formation (ramet cost).

Initial ramet size and resource

The initial ramet resource after branching or lateral ramet formation is

$$R_t = (R_{\text{avail}} - C_{\text{i}}) \,.\, f_{\text{g}}, \qquad (6)$$

where R_{avail} is the value defined by eq (4), C_{i} is the internode cost, and f_{g} is the proportion of resource put into the new ramet at the growing tip. This is identical also for branching and primary rhizome formation (in such a case the value of C_{i} is multiplied by number of nodes on the primary rhizome). When a ramet is formed, it retains the resource put into it as an 'endowment'. (In contrast, building of an internode leads to a net decrease of the resource by subtraction of C_{i} .)

Ramet size after branching or lateral ramet formation is set to

$$x_t = x_{\text{init}} + r_{\text{c}} \,.\, R_{\text{tip}} \,.\, (K_{\text{c}} - x_{\text{init}}) / (1 + \alpha \,.\, R_{\text{tip}}) \qquad (7)$$

where R_{tip} is the initial resource of the newly formed ramet, x_{init} is the initial ramet size after seedling establishment (parameter *init_size*), K_{c} is the maximum ramet size for that species, x_{init} is the initial ramet size. This expresses the dependence of the initial ramet size on resource available using the same approach as used in Eq (1); the higher the resource available in the rhizome when a branch with a ramet or a lateral ramet are formed, the bigger the ramet will be.

Condition for branching

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

$$R_{avail}' > C_i + R_{min} / f_g \qquad (8)$$

distance to the previous branch is greater than a specified value (*br_allowed*)

where R_{avail}' is the value defined by eq (4) reduced by the cost of producing terminal ramet and the internode (following equation (6), i.e. $R_{avail}' = (R_{avail} - C_i) . (1 - f_g)$), C_i is the internode cost, R_{min} is the minimum resource required for ramet formation, and f_g is the proportion of resource put into the new ramet at the growing tip.

NB. If branching takes place, the new branch is formed at the angle that is drawn from a Gaussian distribution with the mean *branch_angle* and standard deviation *sd_angle.* Angle is always defined relative to the direction of branch bearing node and the previous node.

Condition for primary rhizome formation

Primary rhizome is formed instead of usual terminal growth with a specified probability (parameter *freq_n_primary*) if the photosynthetic balance of the ramet is likely to be negative:

$$(1 - \beta . N) < 0 , \qquad (9a),$$

or with another probability (parameter *freq_p_primary*) if

$$(1 - \beta . N) >= 0 , \qquad (9b),$$

Always the tip has to have sufficient resource, i.e.

$$R_{avail} > n_p . C_i + R_{min} / f_g \qquad (9c),$$

where R_{avail} is defined by equation (4), R_{min} is the resource required to produce a ramet, β is the density-dependence constant of resource accumulation for that species, n_p is the number of nodes in the primary rhizome, C_i is the internode cost, f_g is the proportion of resource put into the new ramet at the growing tip, and N is the sum of ramet sizes of all neighbours of that ramet. A simplifying assumption is made that the cost of a node can be approximated by the internode cost if there is no ramet on the node. When primary rhizome formation takes place, n_p nodes are produced during one plastochron; their internode length is r * *length_primary* (definitions see below). If a primary rhizome is formed, the terminal ramet is changed into a lateral one and a new ramet is added at the tip of the primary rhizome.

Condition for lateral ramet formation

Lateral ramet is formed with a specified probability (parameter *prob_lateral*) if the following condition is met:

$$(1 - k . \beta . N) > 0 \qquad (10)$$

$$R_{avail} > R_{min}$$

node age is smaller than a specified value (*nodes_alive*) where R_{avail} is defined by equation (4), R_{min} is the resource required to produce a ramet, β is the density-dependence constant of resource accumulation for that species, k is a positive constant and N is the sum of ramet sizes of all neighbours of that ramet. The second part of the condition assures that ramet is formed only when it is likely to have a positive photosynthetic balance (i.e. when $N >> 1/\beta$). The constant k determines the 'readiness' to form a new ramet once the photosynthetic balance would be positive in the current step; if it equals 1, then the ramet then ramet is formed always if the current balance would be positive (i.e. $N > 1/(\beta\ .\ k) > 1/\beta$ for $k > 1$); values greater than one mean that the expected balance should be at a certain threshold for the ramet to be formed. Lower values tend to produce oscillations in ramet number (due to the lag effect of synchronous updating of all ramet sizes); higher values act as a buffer. It is fixed to 2 in the current implementation.

NB. R_{avail} is calculated independently for lateral ramet formation and sleeping bud activation. One value is calculated first for terminal nodes only (using the Eq. (4)) for terminal growth (both primary and secondary)and terminal branching. Then another value is calculated based on the remaining resource for each node (proceeding basipetally); this value is used for lateral ramet formation and sleeping bud activation.

The decision of ramet formation is done at each node at each plastochron over the whole lifetime of the node (the lifetime is determined by the rhizome fragmentation due to node death, determined by the parameter *nodes_to_die*). This differs from the processes of terminal growth and branching, where the decision is made only once – when the node is terminal. As a result, even moderate values of *prob_lateral* will produce rhizomes almost fully occupied with ramets if combined with lifespan values not being very close to 1. On the average, the proportion of nodes bearing ramets is $p\ /\ (p + 1/l)$, where p is *prob_lateral* and l is *lifespan*. For example, values of these two parameter being 0.01 and 20 will yield approx. 17% of nodes being occupied by ramets; 0.1 and 10 will yield approx. 50% nodes being potentially occupied. (This is, however, stronlgy modified by neighbourhood conditions of lateral ramet formation and resulting resource levels if competition is intense.)

Condition for ramet death

A ramet dies if its resource calculated by equation (2) is <= zero (i.e. its photosynthetic balance is negative). Note that this kills immediately all ramets with negative balance if there is no resource retained ($S = 0$) and no translocation ($T = 0$). The same process applies to non-clonal plants, lateral ramets and terminal ramets.

For lateral ramets, there is an additional criterion based on age: it dies after number of plastochrons drawn (for each ramet separately) from a gamma distribution with mean of *lifespan* and variation coefficient of *cv_life*. NB. If the parameter *cv_life* is close to 1, it may happen that the expected lifespan for that ramet will be zero and the ramet will die at the same plastochron as it is formed. No tests are done to prevent this.

Ramets may also die as the result of density-independent stochastic mortality.

Ramet radius

If ramets have non-zero radius (if *diam_a* > 0 for all species), it is calculated at each step from ramet size using a simple allometric formula of the following form:

$$\text{radius} = a \,.\, x^b \qquad (11),$$

where x is the ramet size and a and b are constants. Radius calculated using this formula is used to define zones of influence and their overlap (formulas 3a or 3b).

Condition for basipetal node death

A node dies if its age (ie. current time step time minus step of its formation) exceeds a specified constant (*nodes_to_die*). If a node dies it disappears with the attached ramet and internode. If it bears a branch, rhizome fragmentation occurs.

A node ceases to be active (i.e. to produce ramets or activate sleeping buds for new rhizome fromation) if its age exceeds a specified constant (*nodes_alive*).

Condition for sleeping bud activation to form a branch

A branch is formed by activation of a sleeping bud is formed with a specified probability (parameter *sleeping_bud*) if the following condition is met:

$$R_{\text{avail}} > R_{\text{min}} + C_{\text{i}} / f_{\text{g}} \qquad (12)$$

distance from the tip is bigger than a specified constant,

where R_{avail} is defined by equation (4), R_{min} is the resource required to produce a ramet, C_{i} is the internode cost, and f_{g} is the proportion of resource put into the new ramet at the growing tip.

A similar caution on frequency holds here as for the lateral ramet formation.

Condition for non-clonal/clonal transition

This can be based either on age or on the resource status (this is defined by the parameter *mode_to_clonal*). If based on age, a non-clonal plant begins to grow clonally when the specified number of time steps have elapsed from its establishment; if based on resource, it begins to grow clonally of the resource exceeds a certain limit. This limit is specified in the variable *criter_to_clonal*, it changes meaning depending on the value in *mode_to_clonal.* If the criterion equals zero, the plant begins to grow clonally immediately after establishment.

A non-clonal plant may form one or several branches/rhizome fragments. This is determined by the parameter *how_many_clonal.* The number of rhizome fragments formed is $1 + x$, where x is drawn from the Poisson distribution with the mean given by *how_many_clonal* – 1. This yields one branch if *how_many_clonal* = 1 and never attains zero value.

Distance and angle of growth

When a new node is added, it is formed at a distance from the current terminal node drawn from the gamma distribution with the mean r and standard deviation $r * cv\_r$ (i.e. parameters of the gamma distribution being $\alpha = 1/(cv\_r)^2$ and $\lambda = \alpha / r$). The angle of the newly formed internode with the previous internode is drawn from the Gaussian distribution with the mean zero and standard deviation *sd_angle*. The left/right decision is made either based on the density of ramets surrounding the newly formed node (if *bra_orient* = 0) or the angle closer to 180^o is taken (if *bra_orient* = 1)

The same applies to branches except that the mean angle for branching is *branch_angle*; see also the note at the 'condition for branching' section.

Angle of a newly formed clonal plant (from the seedling or by nonclonal-to-clonal transition) is either random (if *start_orient* equals 0) or 180^o (if *start_orient* equals 1).

Temporal variability

Temporal variability can be introduced for the resource accumulation rate (A). In such a case, after *stp_accum* steps (a species-specific constant) a value of A is drawn from the gamma distribution with the mean *accum* and coefficient of variation of *cv_accum*. The environmental change is done for each species independently. If *stp_accum* o r*cv_accum* are zero, there is no temporal variability in accumulation rate.

Seedling establishment

At the beginning of a simulation, *no_isr* seedlings are distributed randomly in the plane. Their initial size is x_{init} and their initial resource is R_{init} (by definition is 1). Angle of a newly formed clonal plant (from the seedling or by nonclonal-to-clonal transition) is either random (if *start_orient* equals 0) or 180^o (if *start_orient* equals 1).

At each later step, *no_rsr* seedlings are distributed randomly in the plane with the settings identical to the initial seedlings.

Correlated density independent mortality of ramets (fire, disturbance)

If the time step equals *fire*, the aboveground ramets die with the probability of *fsurv*. For these ramets, all the aboveground parts of the plants (ramets) are deleted and the resource levels at each node bearing ramet are reduced by *flost_res* (a species-specific constant). The remaining ramets are unaffected, but their resource is reduced by *flost_res* as well. No resource reduction takes place at nodes with no ramets. Presence of meristems along the rhizome is unaffected, but they have to be activated using the parameter *sleeping*.

Model parameters

For each species the model requires the following parameters. While the number of parameters looks horrifying, it should be kept in mind that not all of them have to be used in the single simulation: all of them are needed only if the species has to display all possible types of behaviour that the model is able to account for.

Name	**Type*)**	**Units**	**Definition**
(1) establishment and non-clonal growth parameters			
no_isr	*float*	genet/time	number of new rhizomes put in the plane at the beginning. Fractional values will lead to a stochastic process with the average given by the value of *no_isr*.
no_rsr	*float*	genet/time	number of new rhizomes put in the plane at later time steps
mode_to_clonal	*integer*	*switch only*	determines how the species shifts from nonclonal to clonal growth; 1 or 3- on the basis of resource, 0 or 2 - on the basis of time steps. The value used (either critical resource, or critical time step) is in variable *criter_to_clonal*. Values 2 and 3 determine that the non-clonal plant stays there and the rhizome is added; values 0 and 1 determine that the non-clonal plant disappears and moves to the rhizome tip.
criter_to_clonal	*float* (ts) **)	time or biomass	determines how may timesteps a plant stays at its original position after establishment if *mode_to_clonal*=0 or 2; determines critical ramet size for clonal growth if *mode_to_clonal*=1 or 3.
how_many_clonal	*float*	rhizomes	how many branches are formed from a non-clonal plant. The number of branches is 1+x, where x is drawn from the Poisson distribution with a mean given by *how_many_clonal* - 1.
start_orient	*integer*	*switch only*	1 if initial growth is always downslope (conventionally slope = 180o); 0 for random initial growth
(2) Size growth and resource dynamics			
r_nonclonal	*float* (ts)	1/time	growth rate for nonclonal plants
K_nonclonal	*float*	biomass	maximum ramet size.
r_clonal	*float* (ts)	1/time	r_c , growth rate for ramets on clonally growing rhizomes
K_clonal	*float*	biomass	$K_{c,}$ K for lateral ramets
init_size	*float*	biomass	x_{init}, size of the ramet establishing from seed. This constant determines relative ramet sizes when there are more species
diam_a	*float*	length /	a, a scaling constant which transforms

		biomass	ramet size into ramet radius (zone of influence)
diam_b	*float*	1	b, an allometric constant which transforms ramet size into ramet radius (zone of influence)
accum	*float* (ts)	1/time	A, constant of resource production during one time step (meaning: *accum* – 1 means how many new ramets a ramet would be able to form per one time step under no-competition conditions)
stp_accum	*int* (ts)	time	after how many time steps the constant A changes value (0 – no variation in A)
cv_accum	*float*	1	coefficient of variation of A.
res_retained	*float* (ts)	1/time	S , 'resource retained' constant (expresses how much of the resource from the earlier step is retained; it should range from 0 to 1, 0 no resource being retained)
res_stored	*float*	1	$f_{c,}$ fraction of the resource not used for the size growth
alpha	*float*	1 / resource	α, determines dependence of the growth rate on resource available. Caution: If it is too small, divergent behaviour will take place instead of convergence to K.
beta	*float*	area	β, strength of density dependence of a species for resource accumulation. This constant determines actual branching rate of rhizomes and mortality of ramets
dens_indep	*float* (ts)	1/time	probability of density independent mortality of a ramet. It is expressed per time step, to be consistent with mortality due to negative photosynthetic balance which takes place (as all growth-related processes) at each time step. NB. Lifespan mortality is expressed per plastochron.
(3) rhizome growth and translocation			
sharing_range	*integer*	nodes	T, range of physiological integration
prop_shared	*float*	1	f_{tr} , fraction of the resource translocated; rest is available at the node of its production for the growth of lateral ramets and translocation in next steps at the original node
p_trans_node	*float*	1	sink strength of a non-ramet bearing non-terminal node relative to a ramet-bearing non-terminal
p_trans_tip	*float*	1	sink strength of a ramet-bearing terminal node relative to a ramet-bearing non-terminal

p_basipet	*float*	1	proportion of resource translocated basipetally
cost_trans	*float*	1/node	C_T , fraction of the resource that is lost when translocated over one node
internode_cost	*float*	resource	C_i , cost of adding one internode to add a terminal node or a branch
fr_res_tip	*float*	1	$f_{g,}$ fraction of the resource available to the node that is put into the growing tip or ramet (after subtracting the cost of the internode production)
flost_res	*float*	1	resource lost by density-independent mortality (fire) in ramet-bearing nodes
fsurv	*float*	1	probability that a ramet dies as the result of density-independent mortality (fire)
(4) rhizome lengths and branching			
steps_per_plast	*integer* (ts)	time	how many time steps per plastochron.
r	*float*	distance	mean internode length
cv_r	*float*	1	variation coefficient of the internode length
sd_angle	*float*	angle	standard deviation of the angle of rhizome growth in degrees. NB mean angle is the angle of the previous time step
nodes_to_die	*integer* (pl)	nodes	after how many plastochrons the basipetal node dies
nodes_alive	*integer* (pl)	nodes	after how many plastochrons the basipetal node loses the capacity to bear lateral ramets
br_allowed	*integer* (pl)	nodes	architectural constraint for branching: how many nodes after an earlier branching it may branch again, provided resource is sufficient.
prob_term_br	*float* (pl)	1/time	probability of terminal branching after it is allowed. If set to 1, branching is driven only by resource available and architectural constraint given by *br_allowed*
branch_angle	*float*	angle	angle of rhizome growth after branching in degrees
bra_orient	*integer*	*switch only*	1 if branching is always done downslope (conventionally slope = 180o); 0 for ’smart’ branching (based on density)
length_primary	*float*	1	relative length of an internode of a primary rhizome. It is expressed as primary/ordinary ratio
freq_n_primary	*float* (pl)	1/time	probability that a tip will form a primary rhizome instead of the ordinary one under

			the conditions of negative photosynthetic balance (high crowding) provided the resource is sufficient.
nodes_primary	*integer*	nodes	n_p , number of nodes on the primary branch - this number of nodes is formed during one plastochron
freq_p_primary	*float*	1/time	probability that a tip will form a primary rhizome instead of the ordinary one under the conditions of positive photosynthetic balance provided the resource is sufficient.
sleeping_bud	*float* (pl)		probability of a sleeping bud forming a branch
(5) Lateral ramet formation			
prob_lateral	*float* (pl)	1/time	probability that a sleeping bud will form a ramet (provided resource is sufficient)
lifespan	*integer* (pl)	time	mean life span of a lateral ramet
cv_life	*float*	1	cv. of life span of a lateral ramet; if != 0, ramet life span has a gamma distribution and a mean given by *lifespan*; if ==0, ramet life span has no variation
(6) Non-species specific parameters			
neighb_size	*float*	distance	D, radius of the neighbourhood size. Must not exceed 0.2. Is not effective when plants are of non-zero diameter (then competition is evaluated using overlaps of zones of influence
deg_asym	*float*	1	θ, is the constant of competitive asymmetry: 0 means perfect (size-independent) symmetry, 1 means perfect size-symmetry and >1 means size asymmetry; ∞ means complete one-sided asymmetry
fire	*int*	time	after how many steps density-independent mortality of the whole stand occurs.

*) If a floating decimal point number is forced into an integer variable, unexpected results may occur.

) **pl refers to constants where time is expressed in plastochrons; **ts** to constants where time is expressed in time steps.