A simple model for the influence of habitat resource availability on lateral clonal spread

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Plant clonal spread is ubiquitous and of great interest, owing both to its key role in plant community assembly and its suitability for plant behaviour research. However, mechanisms that govern spreading distance are not well known. Here we link spacer costs and below-ground competition in a simple model of growth in a homogeneous below-ground environment, in which optimal distance between ramets is based on minimizing the sum of these costs. Using this model, we predict a high prevalence of clonal growth that does not employ spacers in resource-poor environments and a nonlinear increase in spreading distance in response to increasing below-ground resource availability. Analysis of database data on clonal growth in relationship to below-ground resource availability revealed that patterns of the spread based on stolons is compatible with the model’s predictions. As expected, model prediction failed for rhizomatous species, where spacer sizes are likely to be selected mainly to play roles other than spread. The model’s simplicity makes it useful as a null model in testing hypotheses about the effects of environmental heterogeneity on clonal spread.

1. Introduction

Clonal plants are frequently the dominant guild in terms of both biomass and number of species. In temperate areas, their relative abundance with respect to non-clonal plants is greater in less productive habitats [1], which may indicate a possible relationship between habitat productivity and selection for clonality. Among clonal plants, the majority of species spread by stem-derived spacers, located either below-ground in the form of rhizomes or above-ground as stolons, reaching distances that span over an order of magnitude [2]. Selection seems to have influenced the spreading distance, as some general trends link higher environmental productivity with farther lateral spread [3,4], although this relationship bears strong signals of phylogenetic and morphological constraints [3,5]. However, the mechanism underlying the relationship between productivity and spread distance is still not known.

Spread by spacers allows plants to integrate resources across environmental heterogeneities [6,7]. This integration may improve the fitness of the new ramet as an eventual independent individual, or it may increase the level of resources available to the clone as a whole. However, it incurs a cost in the resources needed to make and maintain conductive spacers. This is especially true for stoloniferous plants, as their roots are situated only at the nodes bearing new ramets, with the spacers not self-sustaining. Thus, spread by spacers is an effective strategy in terms of resource acquisition only if the new ramet can be placed such that the net resource income is non-negative [8,9].

The question of ramet placement in intrinsically heterogeneous environments has been the subject of considerable research including experimental studies [10–12] and construction of in silico models (reviewed by Oborny et al. [13]). Surprisingly, much less attention has been paid to understanding ramet placement in intrinsically homogeneous environments, i.e. those in which...
heterogeneity occurs not as the driver, but as the result of the presence of plants at particular locations (yielding self-generated heterogeneity) [14,15].

Here we develop a model of spacer length between two directly connected ramets as a basis for overall lateral spread extent. The model seeks to explain spacer lengths simply in terms of overall soil resource availability and spacer production cost rather than relying upon external environmental heterogeneity. As such, the model may be used as a basis for quantification of plant spreading strategies that frequently deviate from simple maximization of resources in heterogeneous environments [16,17].

Furthermore, we compare the model’s predictions to those yielded by an alternative one based solely on the assumption of overall plant size, including its spreading structures, increasing with soil resource productivity in a unified manner (hereafter referred as isometric model). In this isometric model, both overall plant size and the distance between ramets have the same relationship with environmental productivity, i.e. plants in higher resource environments have greater spreading distances simply as a linear function of greater size of spacers. To differentiate between these two models, we compare clonal plants with two different types of spacers, namely stolons and rhizomes. While both spacer types serve for clonal growth, they differ in their additional functions, with rhizomes being much more often involved in storage and soil resource acquisition in addition to clonal growth [18]. As our model does not take into account these processes, it is likely to hold for stoloniaeforous plants only; by contrast, if response to increasing soil resource availability is based on simple isometry, it is likely to affect both stolons and rhizomes in the same way.

Plausibility of these qualitative predictions of these two models is then compared to the relationships between database values of spatial clonal growth and species optimum along the gradient of below-ground resource availability, assessed by Ellenberg indicator values (EIV) [19].

2. The model

The underlying idea of the model is that spacer length is dictated by the need of the entire interconnected clonal fragment to maximize resource net gain, and for ramets to therefore be located accordingly. While maximum spacer length would then be limited by the cost of the spacer itself, minimal spread distance would derive from the need to avoid potential future competition between mother and daughter ramets. We represented the cost of distance in a ‘common currency’ as resource gain, enabling us to perform additive operations to optimize overall plant performance.

Our model assumes symmetric competition between mother and daughter ramets for below-ground resources [20]. We did not include above-ground competition because of the strong asymmetry that characterizes competition for light, which would result in daughter ramets, necessarily smaller than the mother ramet, being strongly suppressed by shading in the close vicinity of the mother. For the sake of simplicity, we assumed permanently connected mother and daughter ramets of the same final size.

We assumed that the cost of a spacer (S) is linearly determined by its length (spreading distance, D, in metres) and unit spacer cost paid for both establishment and maintenance of the spacer during its lifetime (u, in resource/metre):

\[ S = D \cdot u. \]  

(2.1)

In a given environment, the amount of resource acquired would be determined by the rhizosphere size, with the length of each root optimized for the resource availability: as the root incurs a cost per unit of its length, maximal root length would be limited to that at which it acquires just more than it costs [21–23]. Thus, a more productive environment would lead to bigger plants with bigger rhizospheres.

To keep the model simple, we assumed that the cost per unit root is constant. This would lead to a hemispherical rhizosphere. However, as environments differ in their depths of maximal resource content, and natural selection should act towards maximizing acquisition capacity by the roots at that depth, we decided to instead use a half spheroid (i.e. half an ellipsoid of revolution), with its width-to-depth ratio determined by the depth that contains the maximal amount of the resource. This representation allowed us to include rhizosphere shapes from nearly cylindrical to nearly flat.

We assumed that within the rhizosphere the roots homogeneously extract the resource and that rhizospheres are discrete in space, with sharp boundaries (or very steep gradients) between fully exploited and non-exploited areas. The amount of the resource acquired (A) would thus be proportional to the radius (a) and depth (b) of the spheroid (equation (2.2)), with scaling constant (c) in resource/m³, converting rhizosphere volume to plant extractable nutrients. As a is linearly dependent on b, then b can be interpreted as a scale (size) parameter of the rhizosphere, and \( k = a/b \) as its shape parameter:

\[ A = \frac{2\pi}{3} c \cdot a^2 b. \]  

(2.2)

If ramets are too close to each other (i.e. the distance between their centres is less than the diameter of the rhizosphere), their potential rhizospheres overlap. With overlapping rhizospheres, future clonal fragments would acquire less of the resource than two ramets farther apart from each other (figure 1). We denote the difference in resource acquisition due to rhizosphere overlap as the competition cost (C), i.e. it is the sum of the resources that would not be acquired because of ramets proximity during their life. It is proportional to the volume of the overlap of the rhizospheres, which can be calculated as an ellipsoidal side cap volume of height \( a - D/2 \) as follows:

\[ C \approx \int_{x>D/2} \frac{b}{\sqrt{a^2 + x^2 + y^2}} dx dy \]

\[ = 2\pi a^2 b \left( \frac{1}{48} \left( \frac{D}{b} - 2 \right)^2 \left( \frac{D}{b} + 4 \right) \pi \right) \]  

(2.3)

for \( 0 < D < 2a \).

The overall loss (T) in the capacity to gain the resource is then the sum of both costs:

\[ T = cC + S, \]  

(2.4)

and it relates to the spreading distance

\[ T = \frac{ca^2 b \pi}{24} \left( \frac{D^3}{b^5} - 12 \frac{D}{b} + 16 \right) + Du. \]  

(2.5)
between the rhizosphere size reflecting environmental productivity and the optimal spreading distance approaches linearity (figure 3).

Furthermore, higher unit spacer cost will yield more pronounced curvature of this relationship (figure 3). Different kinds of spacers vary in form and function [24], and therefore also probably vary in the unit cost. This would lead to spacer type-specific relationships between lateral spread and environmental productivity.

Additionally, if the distribution of below-ground resources differs between environments (e.g. persistently wet soils versus arenaceous soils with water available only in upper horizons after rain), this would affect the shape of the rhizosphere. Plants with different rhizosphere geometry will differ in optimal spreading distance, with the relationship between rhizosphere shape and this distance not necessarily monotonic (figure 4).

4. Testing the model

(a) Data

As a test of our model, we analysed the relationship between resource richness and spacer distance as shown by growth data from a plant clonal trait database [25] and EIV [19] for soil moisture and nutrient availability. From the database, we selected terrestrial (i.e. EIV for moisture less than 10) species that produce overlapping, physically connected generations using stolons, hypogeogenous rhizomes or epigeogenous rhizomes. Hypogeogenous rhizomes are produced below ground, whereas epigeogenous rhizomes originate above ground, but with the distal portion typically situated beneath soil or litter [25]. The unit stolon cost is sometimes considered lower than the cost of rhizomes [26], also rhizomes are more often built to last longer than stolons and serve functions other than spread (namely storage). We considered all of these spacer categories both together and separately. If a given species was listed as using more than one of these different spacer structures, we would input the relevant data for the species and test the model for each of these spacer categories. Lateral spread distance was coded as an ordinal factor having three possible levels, as presented in the database: less than 1, 1–25 and greater than 25 cm. Availability of EIV as values characterizing the most common habitat for particular species limited the testing species pool to Central European species.

(b) Methods

Because both the EIVs and lateral spread values are on ordinal scales, we used Kendall’s τ rank correlation coefficient as a measure of the association between the resource levels and the lateral spread values. Calculations were done using the cor.test procedure available in the stats package of the R statistical environment (v. 2.11.1, [27]). We estimated probability levels of null hypotheses using one-sided tests, because, according to our model, lateral spread would be greater in richer environments.

(c) Results

When considering the whole dataset, positive relationships between lateral spread and resource availability were apparent, as predicted. While the relationship between spread and water availability was highly significant ($p < 0.01$), it was less so in the case of the spread-nutrient availability relationship.
In both cases, the associations were rather weak (table 1).

When the dataset was analysed separately by spacer type, substantial, significant positive associations between both water \((p = 0.014)\) and nutrients \((p < 0.001)\) and lateral spread were found for stolon-based spread. There were no significant positive associations between rhizome length and below-ground resource availability (table 1 and figure 5).

5. Discussion

We predicted that plants which spread by spacers would occur in relatively resource-rich environments, compared to root splitters. This was based on our inference that in extremely poor environments, even the small cost of the minimal usable spacer would need to be avoided, with other strategies to avoid local competition preferable. A study of the relationship between clonal plant spacer types and various habitats, using largely the same data to those we employed, revealed this prediction to be well supported (see Van Groenendael et al. [4] for additional support of our hypothesis).

In our study, when all the plants were considered together, the distance of lateral spread increased with the availability of below-ground resources in the environment, as predicted by our model, although the effect size was rather small. However, this qualitative outcome would also be predicted by simple isometry. The crucial distinction between the outcomes generated...
by the two models is that the former would yield a nonlinear relationship, and the latter, a linear one. While the existing data do not allow direct assessment of linearity to distinguish the form of the response, additional features of the model can help separate these two potential mechanisms.

In simple isometry, lateral spread distance would not be influenced by unit spacer cost, thereby yielding the same relationship between lateral spread and below-ground resource availability for all spacer types. By contrast, our cost-based model would produce different outcomes according to spacer types and their unit costs. The data showed that lateral spread based on different spacer types differed in their relationships to below-ground resource availability, thus providing support for our model, while indicating that lateral spread distance was not governed by simple isometry. In particular, the overall relationship we found between water availability and lateral spread was mainly driven by stolon-bearing plants, and these plants showed a positive relationship

**Figure 5.** Relationships of clonal spread distances to environmental gradients, grouped by spacer type. Spread distances are categorized as less than 1, 1–25 and greater than 25 cm. (a) Indicate relationships to moisture and (b) indicate relationships to nutrient availability.

**Table 1.** Associations of below-ground resource and spacer lengths of clonal species categorized by spacer type. (Kendall’s correlation coefficients (r), probability levels of corresponding null hypotheses (p), and number of available species data per category (n) are shown both for moisture and nutrients, as indicated by EIV.)

<table>
<thead>
<tr>
<th>type of spacer</th>
<th>moisture</th>
<th>nutrients</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>r</td>
</tr>
<tr>
<td>all</td>
<td>1014</td>
<td>0.07</td>
</tr>
<tr>
<td>stoloniferous</td>
<td>115</td>
<td>0.174</td>
</tr>
<tr>
<td>epigeogenous rhizome</td>
<td>663</td>
<td>0.032</td>
</tr>
<tr>
<td>hypogeogenous rhizome</td>
<td>236</td>
<td>-0.095</td>
</tr>
</tbody>
</table>
not just between water and lateral spread, but also between nutrients and lateral spread. Rhizomatous plants, which possess more costly spacers [26], did not manifest these relationships. This could be owing to the predicted strong curvatures in the relationship between resource availability and lateral spread for species that employ costly spacers.

On the other hand, the lack of a relationship between resource availability and lateral spread in the two groups of plants that employ rhizomes (epigeogenous and hypogeogenous) is likely to be due to the different nature of rhizomes. Unlike stolons, rhizomes frequently serve both as structures to achieve spreading and as storage organs [24,28] and are built to last [5]. The roles of rhizomes other than spreading may pose functional and geometrical constraints that limit their spreading capacity, but may be vital in environments and life histories in which storage capacity is important [18], subjecting rhizomes to other evolutionary pressures [18,29]. This limitation could make our model inadequate for consideration of spread by rhizomatous plants but should not occur under the isometric model. Stolons are essentially only for clonal spread and support of young ramets [24,18] (but see [30,31]); therefore, stolon-based spread fits perfectly into our modelling framework. Dong & de Kroon [26] performed an experimental study on this issue, and their results are in accord with our prediction and argumentation: in their experiment, plants generated shorter stolons in low-nutrient treatment compared with high-nutrient treatment, whereas rhizome length was unaffected. We suggest that our hypotheses can be tested by further experimental studies, preferably on stoloniferous species. Directly manipulated resource availability as well as spacer cost estimation would allow us to discriminate between our model and isometry in lateral spread of clonal plants.

An additional prediction of our model shows that even in a horizontally homogeneous environment, rhizosphere shape may have a profound effect on the optimal spreading distance. Moreover, rhizosphere shape is likely to vary in accord with the vertical heterogeneity of the environment [22,32], and vertical heterogeneity of the environment is likely to differ across the broad scale we used for testing the model. Furthermore, innate differences in rhizosphere shape between species from various phylogenetic clades [33] could also influence the outcome of a study such as ours, that examines multiple species across different habitats. To account for such variation, it would be necessary to collect new and compile already available rhizosphere shape data.

(a) Limitations of the model
Our simplifying assumptions fell into two categories. The first category comprised conceptual assumptions essential to building an intentionally simple model, in which the only environmental heterogeneity was self-generated, horizontal and below-ground environment. Our model used the idea of Sachs et al. [34], viewing the plant both as a single body and as a population of competing organs at the same time. The model’s simplicity allows its usage as a null model in testing hypotheses concerning the effects of phenomena such as external heterogeneities and competition with other individuals on ramet placement and vegetation composition. So it allows detection of ramet placement strategies that occur in such environments, e.g. foraging [16].

The second group of simplifications was done to ease model construction and decreases the number of parameters needed. Among them, we see the following four as those needing specific attention: (i) rhizospheres rigid in shape, i.e. not adjusting according to the presence of roots of sibling ramets; (ii) initial asymmetry in size between ramets; (iii) rhizospheres discrete in space, with boundaries (or very steep gradients) between fully exploited and non-exploited areas; and (iv) stolons only transporting input, with some constant amount lost per unit length. We discuss each of these limitations below.

First, regarding rhizosphere shape rigidity: in nature this assumption is not met, as plants can adjust rhizosphere shape in response to the presence and identity of neighbours [35,36], e.g. to minimize overlap with siblings [37]. However, this shape adjustment incurs a cost for the plant, as isolated ramets develop non-adjusted rhizosphere shapes. In other words, the shape of rhizospheres is adjusted to neighbour ramets when needed because it is suboptimal for individual ramets. Incorporation of rhizospheres with a plastic shape response to competition into our model would thus require parametrization of the cost and would necessarily lead to less general models, moreover using a parameter of unknown properties [38]. Importantly, this additional parameter would only modify the cost of competition and would not alter the model’s logic.

The second problem is closely related to the first one, as it partly deals with the rhizosphere shape. It could be assumed that at the moment of rooting, the younger ramet from a pair has no rhizosphere and therefore can be placed at the margin of the depletion zone of the older ramet without incurring competition cost. Growth of the younger ramet’s rhizosphere is then possible by two means. Either the younger ramet develops a distorted rhizosphere and pays the above-mentioned cost, even propagating this cost to the next generation, or it has to pay a high cost for competing with its parent in the future. Shorter spacer (lower spacer cost) needs to be balanced with the sum of competition costs increasing over time. While this can be accommodated in the model, more parameters would be needed. This would make the model more complicated and possibly less useful as a simple tool for exploring strategic and behavioural patterns of ramet placement.

Third, the assumption of discrete rhizospheres that are exploited uniformly is unlikely to be strictly satisfied in nature. Indeed, the intensity of exploitation is likely to be uneven within the rhizosphere due to below-ground resource diffusion and branching allometries [21,38]. In particular, real rhizospheres may be exploited more in their centres, and depletion zones for individual resources can vary. Moreover, as resources differ in their migration rate through the soil matrix, these depletion zones may be resource-specific in size, internal spatial structure, stability and time to reach the replacement-depletion equilibrium. However, incorporating these more exact representations would not lead to qualitatively different results and would merely provide scaling variables for different models of the rhizosphere. According to Liebig’s Law, one particular soil resource is appropriate for any given situation, and resource-specific functions and constants may be involved in the model at the expense of its simplicity and general applicability.

Finally, in choosing a linear relationship between spacer length and cost, we also considered the possibility that the cost could be proportional to the transported amount, and
the relationship therefore exponential. Spacer cost estimation, which would be needed to address this issue, has been done only rarely, with inconclusive results (e.g. [15,39–41]). We chose the linear relationship because it has the same main attributes and a simpler form than the other option. An exponential relationship would increase the rate of growth of the spacer cost, which would limit the maximal spread more strongly and change the shape of the placement function. However, its general properties (a single minimum of total cost) would not be altered. An exponential relationship of spacer length and its cost would probably increase the curvature in the optimal spreading distance–environment productivity relationship.

(b) Conclusion and implication

Limitations in the test of our model are due mostly to the nature of the available data. Experiments directly manipulating resource levels, performed both within and across species, would be welcome, as the first type would allow control for phylogenetic signal and the second enable assessment of effects of innate differences in rhizosphere shape and unit spacer cost. Phylogenetic signal is strongly pronounced in variability in unit spacer cost [3]. Experiments across species could help to quantify this cost, and particularly to evaluate for rhizomes, the most common spreading structures [25], the influence of roles other than spreading. Additionally, we believe that compiling and analysing case studies on root distributions in various environments both within and across taxa [22,33,42] can yield insights into environmental effects on clonal plant spacing, as mediated by rhizosphere shape.

Although our model could best be tested through manipulative experiments, its simplicity makes it more broadly useful as a null model against which to test hypotheses based on system attributes, such as intrinsic environmental heterogeneity, that it explicitly excludes. Therefore, it may be used in testing the presence of clonal growth strategies such as foraging or clumping [16]. Far spreading fast moving plants are beyond the capacity of the model, as they leave the patch before stable rhizospheres develop [16]. In those cases, the model could only estimate an upper bound of the spread.

We believe that the main ideas underlying our model (modularity of plant body resulting in possible self-competition and resulting selection to diminish total costs) are general enough to be applied to many more systems dealing with plant growth, including positioning of above-ground parts. Such systems are numerous, with clonal spread being especially subject to recurrent investigation in plant ecology [13,43,44]. The particular example that we examined lies at the intersection of two areas of interest in plant ecology: the role of ramet positioning in small-scale vegetation composition [45–48] and ramet placement plasticity and its effect on plant behaviour [10,49,50]. Our model can serve as a suitable null model of ramet positioning to test hypotheses regarding environmental effects, enabling further inquiry into both of these topics.

Data accessibility. Data for model testing are publicly available [19,25].

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Author contributions. M.W. formulated the idea and drafted the model, compiled the data for testing and tested the model, drafted the manuscript. J.S. formalized the model, thoroughly and critically reviewed the draft in several rounds. Both authors gave final approval for publication.

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