Roots in space: a spatially explicit model for below-ground competition in plants

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Game theory provides an untapped framework for predicting how below-ground competition will influence root proliferation in a spatially explicit environment. We model root competition for space as an evolutionary game. In response to nutrient competition between plants, an individual's optimal strategy (the spatial distribution of root proliferation) depends on the rooting strategies of neighbouring plants. The model defines and predicts the fundamental (in the absence of competition) and realized (in the presence of competition) root space of an individual plant. Overlapping fundamental root spaces guarantee smaller, yet still overlapping, realized root spaces as individuals concede some but not all space to a neighbour's roots. Root overlap becomes an intentional consequence of the neighbouring plants playing a nutrient foraging game. Root proliferation and regions of root overlap should increase with soil fertility, decline with the distance cost of root production (e.g. soil compactness) and shift with competitive asymmetries. Seemingly erratic patterns of root proliferation and root overlap become the expected outcome of nutrient foraging games played in soils with small-scale heterogeneities in nutrient availability.

Keywords: root interactions; root allocation; competition; spatial root distribution; game theory; Tragedy of the Commons

1. INTRODUCTION

Lateral root spread and overlap in root systems dictate a plant's ability to acquire below-ground resources and its interactions with neighbours (Fitter 1994; Casper *et al.* 2003) and is thus an implicit factor in determining many of our modern cultivation techniques. Despite the ubiquity of overlapping roots between plants, few models explain how plants distribute their roots in space in response to competitors. Predictions of lateral root spread for individual plants either assume decreases with distance due to declining uptake efficiencies (Weiner 1984; Pacala & Silander 1987) or apply allometric (sized based) equations derived from empirical data (Schenk & Jackson 2002; Casper *et al.* 2003). While such approaches are successful in predicting the root distributions of an isolated plant, they do not account for interactions with neighbouring plants. Recent theoretical approaches based on cost–benefit analyses have generated sometimes contradictory predictions about root distributions, including overlap avoidance, equal division of resources and 'over' production of roots in shared spaces (Novoplansky & Cohen 1997; Gersani *et al.* 1998, 2001). While these spatially implicit models have generated useful predictions, making them spatially explicit, expands their predictive power and may reconcile some of these discrepancies. A spatially explicit model permits investigations of factors such as neighbour proximity and heterogeneous resource distributions. Here, we extend the spatially implicit Tragedy of the Commons root model of Gersani *et al.* (2001) to spatially

explicit environments. The model predicts the explicit distribution of two plants' root systems in response to their proximity, the heterogeneity of resources and the plant-specific fixed and distance costs of producing roots. By predicting the degree of root overlap between two neighbouring plants, we can identify two key regions: a plant's *fundamental root space*, where it would grow roots in the absence of a neighbour and its *realized root space*, where it grows roots in the presence of a neighbour.

Gersani *et al.* (2001) modelled root competition between neighbours as a nutrient foraging game. In their model, an individual's fitness (G) depends not only on its production of roots (v), but also on the amount of roots produced by other plants (u) and the number of other plants (N). The net nutrient profit of an individual is given by the fitness generating function, $G(v, u, N) = (v/x)H(x) - C(v)$, where x is the total amount of roots produced by all plants; $H(x)$ is the amount of nutrient harvested for a given amount of total root production; and $C(v)$ is the cost for a focal individual to produce a given amount of roots. The root production of an individual at the evolutionarily stable strategy is a weighted average of the marginal rate of nutrient uptake of the individual and the average rate of nutrient uptake of all individuals (electronic supplementary material text).

Overlapping root systems produce a Tragedy of the Commons. Though each plant produces fewer roots in a patch than it would if it was alone, the combined root production is greater than merited by the amount of resources. This overproduction of roots produces a Tragedy of the Commons because all plants would enjoy a higher net nutrient profit if they would collectively curtail their root production. However, any given individual suffers if it unilaterally curtails root production.

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Figure 1. (a) shows the fundamental and realized root spaces of two plants in an asymmetric interaction. The red, pink and purple regions are the realized root space of plant two, while the fundamental root space includes these regions as well as the light blue one. The isocline for plant one is the line which separates the purple and light blue regions. Blue, light blue and purple show the realized root space of plant one, while the fundamental root space also includes the pink region. (b) shows the same scenario for a specific spatial arrangement where the plants are four units apart. Distance combinations that are not possible are shaded in black. (c) shows the amount of roots produced by two plants under this spatial arrangement. Warm colours represent greater root density. (d) shows how the regions of the isocline in *b* translate into *xy*-space. The size of each of the regions in *b*, *d* is equal.

In this model, space is implicit. We now extend the model to accommodate the actual spatial arrangement of plants and nutrients with respect to two competing plants.

2. THE MODEL

In the spatially explicit model, the costs of root growth include a fixed cost of producing roots, independent of location, as well as a distance cost of root production that increases with the square of distance from the plant stem. Thus, the total cost of producing an amount of roots, v_i , is represented by $C(v_i) = (c_i + \gamma_i d_i^2)v_i$, where c_i is the fixed cost; d_i is the distance from plant i 's stem; and γ_i scales the distance cost. We designated nutrient uptake for v_i roots as $H(v_i) = R(1 - e^{-av_i})$, where a is the encounter probability (root encountering nutrients and taking them up) and R is the pool of available resources.

The optimal root production for a plant depends on both the distance from its own stem and the distance from the stems of neighbouring plants. A plant's fundamental

root space is defined by the equation, $\hat{d}_i = \sqrt{(aR + c_i)/\gamma_i}$, (electronic supplementary material). In the absence of competition from neighbours, a plant will produce roots at any point which is less than this critical distance from its stem. The fundamental root space of a plant is very similar to field of neighbourhood models (Berger *et al.* 2002).

Root production becomes a game when the two plants' fundamental root spaces overlap. A plant's optimal root production in regions of overlap now depends on the amount of roots an overlapping individual produces. The optimal amount of roots for this other plant depends on the distance from its stem, as well as the amount of roots the focal plant produces. Solving these equations yields the isoclines for plants one and two (Box 1 of electronic supplementary material). These isoclines represent the boundaries of lateral root spread when root systems overlap (Rosenzweig 1981). They illustrate the realized root space of a plant, within which a plant grows roots in the presence of competitors. The realized root space is where our model diverges from the circular zones of influence predicted by

Figure 2. Root overlap under different scenarios. (a) the two plants are identical in both the fixed and distance cost of producing roots. (b) the plants have identical distance cost, but plant two has a higher fixed cost. (c,d) show the effects of resource heterogeneities. In both cases, the average level of resources is the same as in the previous scenarios. (c) there is a resource gradient from the left to the right. Resources increase from the left, where the resource level is zero, to the right, where the resource level is twice what it is in the previous figure. (d) shows an example with heterogeneous resources. Patches have resource levels ranging from zero to eight times the average level, but with the same average resource level as in (a).

some distance models of plant interaction. The ceding of space to neighbouring competitors instead predicts root spreads resembling those of other models. What our model does is allow the spatially explicit competitive interactions (that are also built into field of neighbourhood models) to change the root distribution of individuals and thus potentially alter the interactions themselves, particularly if you scale up to the community. The end results resemble Dirichlet tessellation distributions but also take into account differences among species and show exactly where root systems overlap (Czaran & Bartha 1992). In our model, overlap between root systems becomes a strategy for dealing with competition given the environment in which the interaction takes place and this differentiates it from other spatially explicit models where plants are much more passive including zone of influence, field of neighbourhood and tessellation models (Czaran & Bartha 1992; Berger *et al.* 2002). When a plant does not overlap with any others, its fundamental and realized root spaces are identical.

3. SIMULATIONS

In our simulations, we assume continually renewing resource levels (of a generic nature that could include nutrients and water) although experimentally, this

assumption is not always important (O'Brien *et al.* 2005). Figure 1a,b. illustrates the isolegs. They translate into Cartesian space for a case where two plants have asymmetric costs but identical fundamental root spaces (figure 1c,d). Plant one has lower fixed costs than plant two, but a higher distance cost. Figure 1a depicts the isolegs in the state space of the distance away from the stem of plant one versus the distance from the stem of plant two. The isolegs divide the state space into six distinct regions (table 1) that show how the realized and fundamental root spaces differ in response to overlap with neighbours. Overlapping fundamental root spaces render unprofitable in some areas that would be profitable for root production if a plant was alone. Figure 1a shows at which distance combinations a plant should produce roots. The fundamental root spaces for the two plants are identical. But their isolegs and realized root spaces are not mirror images owing to the cost asymmetries.

For a given distance between two stems, only certain distance combinations are possible. Therefore, we need to know how the plants are arranged in space before we can know how much space each plant cedes to its competitor (figure 1b; non-existent points are shaded black). (see electronic supplementary material for a more detailed description of the effects of neighbour distance.)

Table 1. The six different regions of [figures 1 and 2](#). (Fundamental root spaces are where plants grow roots in the absence of competitor and realized root spaces are plants grow roots in the presence of competitors. These six regions are: (i) white unoccupied areas that are outside of both plants' fundamental root space, (ii) red areas which are only in plant one's fundamental root space, (iii) blue areas which are only in plant two's fundamental root space, (iv) pink areas which are within both plants' fundamental root spaces but are ceded by plant two due to a cost disadvantage, (v) light blue areas within both plants' fundamental root spaces that are ceded by plant two, and (vi) a region of overlap.)

	plant one's fundamental root space	plant one's realized root space	plant two's fundamental root space	plant two's realized root space
white	no	no	no	no
red	yes	yes	no	no
pink	yes	yes	yes	no
purple	yes	yes	yes	yes
light blue	no	yes	yes	yes
blue	no	no	yes	yes

Root production for a given distance between plants can also be visualized in Cartesian space ([figure 1c,d](#); distance between the plants is the same as the isoleg diagram in [figure 1b](#)). [Figure 1c](#) shows the total root production of the pair; warmer colours indicate increasing root production. There are two main peaks of root production in this figure. One peak centres around the stem of plant one as a result of its greater root production. The other occurs in the region of overlap between the two plants. This represents the overproduction of roots that defines the Tragedy of the Commons. [Figure 1d](#) focuses on root spread instead of root density and shows the difference between fundamental and realized root spaces within the Cartesian plane. Plants produce circular root distributions and circular fundamental root spaces when resources are uniformly distributed in space. When their fundamental root spaces overlap, plants concede space and root distributions become more reminiscent of the polygons observed in nature ([Mou *et al.* 1993](#); [Brisson & Reynolds 1994](#)). The region shaded in purple shows the overlap of the realized root spaces of the two plants. Where the plants overlap, they consider the average rate of nutrient uptake which is higher than the marginal uptake rate that they consider when alone (electronic supplementary material). While each plant produces less root in the region of overlap than it would while alone, the total amount of roots produced is greater than would be expected from resources alone ([figure 1c](#)). As mentioned above, this is the region where the Tragedy of the Commons occurs.

4. INTRODUCING NATURE INTO SIMULATIONS

More realistic environments can also be introduced into the simulations. We first consider a baseline scenario with homogeneous nutrients and equal competitors ([figure 2a](#)). The distance between the two plants is 4 units, $a=1$, $R=10$, c_1 and $c_2=1$ and γ_1 and $\gamma_2=0.1$, and the coloured regions are the same as before ([table 1](#)). When the plants have equal costs, their fundamental root spaces are identical, as are their realized root spaces. In nature, it is unlikely that interacting plants are equal competitors. Interspecific interactions are, by their very nature, asymmetric. Inherited and stochastic differences frequently make intraspecific interactions asymmetric as well. Increasing the fixed cost of plant two creates a simple asymmetry and generates a smaller fundamental root space for plant two ([figure 2b](#), $c_2=3.25$). In addition,

plant two cedes proportionally more area to the superior competitor than in the symmetric interaction, while plant one cedes less space. The areas ceded by the two plants are not necessarily equal when the asymmetry is due to different distance costs and thus can create an even larger asymmetry in the interaction in those scenarios.

Resource heterogeneity can also introduce asymmetry into plant interactions. In [figure 2c](#), plants that are identical to those in the baseline case now inhabit a resource gradient that has increasing nutrients from left to right. This resource gradient favours plant two, but both individuals respond by shifting their fundamental root spaces towards the area of higher resource levels. The realized root spaces are similar to those seen in [figure 2b](#), as the smaller plant again concedes proportionally more space ([figure 2c](#)).

The above scenarios still produce largely circular or polygonal root spread diagrams. However, even polygons are an idealization of real root systems because resources are rarely available throughout an environment. The model can examine any resource distribution and when we incorporate highly heterogeneous resource landscapes, our simulated root distributions appear to dramatically diverge from simulations based on more homogeneous resource distributions. [Figure 2d](#) depicts the plants from the baseline case in a world with a patchy distribution of resources. The average level of resources is $R=10$, but individual patches vary from $R=0$ to 80. The analysis only depicts actively foraging roots which creates the 'unoccupied' spaces within the root system, but the cost of these 'missing' roots is subsumed in the general cost of root production. Root spread becomes more like the irregular distribution observed in root excavations ([Weaver & Clements 1929](#)). The $\hat{d}_i$'s and isolegs for resource levels in each patch dictate the root production. However, given that it is advantageous for a plant to grow foraging roots in a profitable patch at a particular distance, it may functionally discount the cost of producing foraging roots in cells of lower values that are en route to the valuable patch. Thus, our model may slightly underestimate foraging root production in small-scale nutrient heterogeneities as a result of this.

The model predicts the conditions under which it is advantageous for plants to proliferate roots into the same space. As a nutrient foraging game, the advantage of proliferating into a patch depends on both the density of roots and the proportion of those roots that belong to

other individuals. In regions of overlap, the plants are predicted to display the Tragedy of the Commons as observed in root competition studies (Gersani *et al.* 2001; Maina *et al.* 2002; O'Brien *et al.* 2005). In any area without overlap, root growth is predicted to match resource availability (Gersani *et al.* 1998). The areas of concession are essentially those predicted by models of root segregation (Novoplansky & Cohen 1997). However, our model predicts that plants will still overlap even when the interaction is highly asymmetric. Experimental evidence supports this (Von Wettberg & Weiner 2003). By being both spatially explicit and game theoretic, our model reconciles some contradictions between existing theoretical and empirical studies.

The predictions generated by our model share quite a bit in common with central place optimal foraging models from animal ecology (Getty 1981; Maynard Smith 1982; Tullock 1983). Simple rules can often lead to complex distributions even when the complication of animal communication is added to the equation (Pacala *et al.* 1996). Adler & Gordon (2003) model the two dimensional foraging area of ant colonies relative to each other and show overlapping foraging effort with each colony ceding space to neighbours based on a cost–benefit analysis. The areas utilized by ant colonies in their foraging efforts resemble the polygons we would expect if our simulations included more than two plants. What is particularly interesting about the Adler & Gordon (2003) model is that they run their simulations with and without conflict. Their simulations resemble ours only when conflict (fighting between individual foragers) is excluded. When conflict is included, the ant colonies are predicted to largely segregate their foraging activities. We draw attention to this as the equivalent in the plant world is allelopathy and this is an aspect of plant interactions that could conceivably be incorporated into our own model at some point.

We can take advantage of existing studies to assess some of the predictions of our model. Fitter (1994) tested for proliferation when two plants were grown in a homogenous environment, comparing isolated plants with those experiencing interspecific competition. Consistent with the predictions from our model (e.g. figure 1d), plants reduced their lateral root spread when a competitor was present. He also found that introducing resource heterogeneity with the addition of fertilizer extended lateral root spread, in accordance with the predictions from our model (figure 2c). The model predicts that plants will grow roots through unprofitable areas to reach patches of high resource availability (figure 2d). Casper *et al.* (1999) found that plants grew roots up to 35 cm away from the base of the plant to access an injected nutrient patch even if some of the areas the plants grew roots through to get to the rich patch were not profitable. Previous models of root production were unable to simultaneously capture all of these different phenomena.

5. CONCLUSIONS

The model we present here provides the conceptual framework for interpreting the results of plant foraging experiments. It makes testable predictions regarding root system overlap, despite black boxing the physiological traits of the plants into uptake and distance-dependent

costs. The model invites extension to more sophisticated models of root architecture. Our model demonstrates that root spread can be predicted by the cost–benefit ratio for root production. In the future, it can be expanded to account for any number of plants with various cost asymmetries and nutrient distributions. Based on the spatially implicit version of the model, simulations with more than two plants should still result in quite a bit of overlap among root systems (Gersani *et al.* 2001). In areas where multiple root systems overlap, the Tragedy of the Commons response should be exacerbated resulting in even greater reductions in reproductive output (*ibid.*). The model's application to existing experiments suggests that a game-theoretic cost–benefit approach can reveal a great deal about root proliferation, root-overlap and below-ground nutrient foraging.

The applied value of this sort of model is potentially rather dramatic. The fundamental root space of any economically important plant can be easily determined experimentally and then compared with its realized root space under a variety of growing conditions. In addition to providing information about the basic ecology of below-ground interactions in plants, applications in agriculture and timber production could save both time and money by generating previously unavailable information on how particular species interact. Without needing to know the detailed physiology and morphology of individual species, comparing fundamental and realized root spaces provide a simple metric of the competitive effect experienced by an individual plant.

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NOTICE OF CORRECTION

The corresponding author's affiliation is now correct.

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