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IDENTIFYING SOURCES OF THE TRAGEDY OF THE COMMONS IN ROOT COMPETITION: A SPATIALLY EXPLICIT SIMULATION MODEL AND PLANTS GROWN IN TRANSPARENT GROWTH MEDIUM

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IDENTIFYING SOURCES OF THE TRAGEDY OF THE COMMONS IN
ROOT COMPETITION: A SPATIALLY EXPLICIT SIMULATION MODEL
AND PLANTS GROWN IN TRANSPARENT GROWTH MEDIUM

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THESIS

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A thesis submitted in partial fulfillment of the requirements for the degree
of Master of Science in the College of Arts and Sciences at the University
of Kentucky

By

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Lexington, Kentucky

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Lexington, Kentucky

2014

ABSTRACT OF THESIS

IDENTIFYING SOURCES OF THE TRAGEDY OF THE COMMONS IN ROOT
COMPETITION: A SPATIALLY EXPLICIT SIMULATION MODEL AND PLANTS
GROWN IN TRANSPARENT GROWTH MEDIUM

Existing research shows that plants produce less root when growing alone than when growing in competition with other plants. When plants under root competition over-allocate resources to roots at the cost of reproduction, it represents a Tragedy of the Commons. I constructed simulation models to determine the circumstances likely to give rise to a Tragedy of the Commons, and explore mechanisms by which plants may solve it. I grew plants in nutrient-rich transparent gel, allowing me to quantify root growth and development without destructive sampling.   My plants responded positively to additional space and the presence of a competitor at full nutrient treatment levels, and negatively to those same conditions between low phosphorus treatment levels, demonstrating nutrient mediation of the direction of plant response to an added competitor with additional space. This effect may feature self / non-self recognition by roots. Since the hard barrier in these studies blocks nutrients, roots, and root signaling compounds from passing between the plants in the barrier treatment level, existing studies cannot tease apart the effects on plant development of these individual factors.   I add a semi-permeable membrane treatment level, which allows nutrients and signaling compounds to pass while preventing root growth between sides.

KEYWORDS: Root, Competition, Tragedy of the Commons, Simulation, Transparent
        Growth Medium

MULTIMEDIA ELEMENTS USED: JPEG (.jpg)

R Deric Leith Miller
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ROOT COMPETITION: A SPATIALLY EXPLICIT SIMULATION MODEL
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ACKNOWLEDGEMENTS

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Chapter 1 – A Spatially Explicit Model of Root Competition

Introduction

A Tragedy of the Commons (ToC) may arise in a broad array of competitive interactions when gains accrue to individuals but costs are shared. Empirical research demonstrates that, under certain conditions, plants competing for soil resources mediated by root uptake may over-invest in root production at the expense of the generation of reproductive mass (Gersani, et. al, 2001). This can produce a ToC because nutrient uptake benefits individual plants but depletes the shared nutrient pool. Yet, if the plants sharing the nutrient pool behaved cooperatively, in the same way that roots of an individual plant behave toward each other, they could each generate more reproductive mass than they do under direct root competition. While existing research confirms that root competition can give rise to a ToC in some systems, other systems do not appear to exhibit ToC effects. Many of the details of the relationship between environmental conditions and the production of a ToC in plant root competition remain unknown.

The (ToC) was originally recognized as a situation in which individual consumers receive short-term benefit from exploiting a common resource, ultimately resulting in over-exploitation to the detriment of all (Hardin 1968). This important concept resonated strongly with emerging environmental awareness when it was first presented (Ciriacy-Wantrup & Bishop, 1975; Fife, 1971), but deeper understanding required the game-theoretic framework increasingly adopted by economists (Clark, 1979; Millinski, et al., 2002), ecologists (Hardin, 1971; Dionisio & Gordo, 2006), and legal scholars (Dagan, H. & Heller, M.A., 2001). As study of the ToC provides insight into fundamental mechanisms of using common resources, it has broad, cross-disciplinary implications. This approach applies to any field that examines the utilization of

resources, including numerous subfields of Biology, Civics, Economics, History, Law, Philosophy, Psychology, and Sociology.

The contemporary scientific effort to explain plant root competition via the ToC begins with an expansion of a model of root proliferation in a heterogeneous resource landscape (Gleeson & Fry, 1997) to considerations of competition (Gersani, et. al., 2001). The earlier paper predicts that a plant should allocate root mass such that the marginal resource gain from each section of its root footprint equilibrate. The study offers empirical support from a grass study in which root allocation increased in relatively nutrient-rich segments of a heterogeneous resource landscape. The subsequent work (Gersani, et. al., 2001) constructs a game theoretic model evaluating the payoffs of building additional root mass to each of two plants sharing a pot. Each plant builds more root until the addition of another unit of root mass would decrease its fitness, according to the equation

$$G(u) = (u/x)H(x) - C(u) .$$

Here G(u) represents the profit that the plant gains from its roots, u represents the amount of root the plant has, x represents the total root mass of all plants, H(x) represents the total nutrient uptake from the landscape (a function of total root mass), and C(u) represents the cost of maintaining the focal plant's roots.

Under this formulation, a single plant will act to balance the cost of maintaining roots with the nutrient gain that they provide. In the single plant case, u = x (the root mass of the one plant makes the total root mass), so the equation simplifies to

G(u) = H(u) - C(u) .

This means that the resource gain from having roots equals the nutrient uptake those roots

provide minus the cost of maintaining them. The single plant seeks to maximize this value, and

will cease adding root mass to its pot once doing so will add more to the cost of root

maintenance than it adds to the benefit provided by the roots.

In the multi-plant case, on the other hand, each plant receives nutrient in proportion to

their share of the total root mass. This bills the other plant for some of the cost of root

investment on the diminishing returns of the investment curve, while the focal plant retains the

benefit. This drives root equilibrium levels of both plants to a higher level, which in turn

decreases nutrient profits, allowing the plants less investment in reproductive mass. As the

number of plants sharing the space increases, this effect will increase.

The equation underlying this prediction determines the Evolutionarily Stable Strategy for

root production under the given profit model:

(N-1) / N * H(x) / x + 1/N * dH/dx = dC/du

When N = 1 (the single plant case), this simplifies to

dH/dx = dC/du

which says that the change in resource removed from the landscape with respect to root

mass equals the change in cost with respect to root mass. The single plant continues to add root,

until additional root costs the plant as much as it benefits the plant, and then it stops. On the other hand, when N = 2, the equation becomes

$$0.5(H(x)/x) + 0.5(dH/dx) = dC/du$$

Here, the plant continues to add root until the average of total uptake per total root mass, plus the change in resource removed from the landscape with respect to root mass, equals the change in cost with respect to root mass. Overall efficiency (dH/dx) now only accounts for half of the plant's decision to stop adding root to the pot. The other half depends on per-plant uptake. As such, each plant continues to add root past the optimally efficient point for utilization of the pot's resource, producing the ToC. As plant count increases, the plant takes increasingly into account the change in average plant uptake in its root production decision, while reducing its response to the change in uptake with respect to root mass (efficiency) into account less and less, increasing the scope of the tragedy.

In support of the predictions of the model, Gersani et al (2001) provide results from a greenhouse study of soybeans: as predicted, plants under competition produced more root mass and less reproductive mass than non-competing plants, holding nutrient available to each plant constant. They observed no significant difference in total plant biomass across treatment levels and instead observed a smaller root/shoot ratio in non-competing plants compared to competing plants.

Since the publication of Gersani et al. (2001), a number of other papers have continued ToC studies with broadening scope and finer resolution. One example expands on the earlier work by directly considering ideal-free-distribution and inter-plant-avoidance alternatives to the

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previous game theoretic approach (Maina, et al. 2002). This work confirms the over-proliferation of root mass and under-reproduction of plants sharing pots, and supports the game theoretic model over the alternatives. In a subsequent expansion of this work (O'Brien, et. al, 2005), researchers develop a three-pot experiment. Here, each of the two plants gets to act as "owner" of one pot, while sharing a third pot, either with or without a dividing barrier. They found that plants over allocate root to the third pot in the absence of a divider (O'Brien, et. al, 2005). Subsequent work suggests that the seemingly erratic patterns of root proliferation come from small-scale nutrient landscape heterogeneity, a claim supported by a spatially explicit model of root growth (O'Brien, et. al, 2007). An empirical study which seems to confirm these results (Hodge, 2003) shows plants allocating more root mass and increasing root ion uptake in nutrient-rich portions of their root footprint, with quantifiable benefit to the plant. A further empirical study (Craine, 2006) posits that the observed high root length density in temperate grasses only makes sense in light of a ToC.

Critics have suggested that the premise of this ToC work has catastrophic flaws due to volume effects and failure to offer adequate empirical support for self / non-self recognition processes (S/NS) (Hess & de Kroon, 2007, Semchenko, et. al, 2007). The concern about S/NS has little merit; the original model, as described above works in the absence of any plant awareness of the competing plant, except indirectly through the second plant's effects on the focal plant's nutrient uptake. The model works solely as a foraging decision, presumably mediated by resource availability, and the presence of the second plant moves the optimal foraging behavior to a less profitable level for each plant (O'Brien, et al., 2007). However, S/NS recognition need not play a role in the ToC. Indeed, if it occurs, it complicates plant competitive behavior in important ways that remain unaddressed by the existing ToC literature (Schenk,

2006).

Criticisms of existing ToC work based on rooting volume concerns have more empirical support (see McConnaughay & Bassas (1991) for a presaging of these concerns). Simply, detractors claim that the ToC effect of greater root growth occurs when a plant has more room to grow in, regardless of the presence or absence of a competing plant. A subsequent response paper directly addresses these objections. The work expands the original game theoretic model to explicitly separate effects of soil volume per plant and per plant nutrient concentration. The new, expanded model makes similar ToC predications to the simpler original. It points out that reproductive mass, not root mass, represents the key variable for measuring the ToC, and this study supports the ToC interpretation of increased root mass and decreased reproductive mass with a fresh series of experiments directly related to space (O'Brien & Brown, 2008).

In the present study I present a simulation model to address these questions and generate new testable hypotheses about the TOC in root competition. How does root competition affect reproductive mass production? What spatial concerns mediate the ToC? What mechanisms can we, as researchers, put in place to limit overproduction of root mass to the benefit of reproductive yield? In the data presented, roots of different plants influence each other only through scramble competition for nutrients; there are no signaling or allelochemical effects or mutualistic benefits between roots of competitors. The simulation permits S/NS recognition as an option, but enabling this recognition did not significantly affect root behavior.

The model allows a non-uniform spatial distribution of nutrients to develop on a two-dimensional grid of square substrate cells, each of which exchanges nutrients by diffusion with its eight immediately surrounding neighbor cells. Each cell loses nutrients to uptake by roots, and gradually recharges its nutrient levels towards a maximum saturation point. I track the

spatial distribution of these roots, nutrients and net uptake by plant competitors under multiple

competitive treatment levels to test means of diffusing the ToC.   These treatment levels include

separating plants with a hard barrier which completely isolates them from one another, and also

separating them with a semipermeable membrane, which allows nutrients to pass freely while

isolating preventing root development across the membrane. Clonal plants will also be

simulated, by giving a single plant, using a single nutrient pool two centers of growth,

representing two clonal ramets, to investigate the relationship between connected clones and the

ToC.

Methods

Formally, the Tragedy of the Commons serves as an example of a contest game, making

it an application of competitive game theory (Dawes et al., 1977). I use a spatially explicit

simulation model to solve the game and generate predictions about the conditions that produce a

ToC, and the extent of ToC effects. I assume that a single soil nutrient (typically nitrogen) limits

plant growth. The model features a heterogeneous resource landscape, so as the simulated plants

draw down nutrient levels, the nutrient diffuses across the landscape down the concentration

gradient. Because the model doesn't simulate above-ground plant structures, nutrient that

remains unallocated to root growth serves as a proxy for reproductive mass. See Appendix A for

full source code.

The simulation model iterates across discreet time steps, and the parameter T_{max}

determines how many time steps the model cycles through before ending. In all of the output

data presented here, the model ran for 500 time steps. In each case this provided the simulated

plants adequate time to reach a stable root structure. The size of the landscape also has a

significant effect on plant behavior. In simulations featuring small boxes relative to the plants'

root footprint sizes, the walls of the box can constrain root growth. The parameters x_{max} and

y_{max} determine the number of cells that comprise the landscape along each dimension.

Each time step consists of a resource dynamics phase in which, first, nutrient resources diffuse

between adjacent cells down the concentration gradient (at a rate determined by the diffusion

constant parameter d). The parameter dcount determines the number of times this phase of the

process cycles for each time step. By setting this parameter to values greater than 1, I model

resource dynamics that operate at a finer time scale than root dynamics. Second, plants take up

nutrients from the landscape. The simulation uses a single nutrient as the mediating currency of

all interactions. Total nutrient uptake across all plants in a given cell in the landscape works

according to the equation $M_{total} = N(1\text{-exp}(-R_{total}))u$ where N represents the current nutrient

concentration in the cell, R_{total} represents the total root mass present in the cell, and u represents

the uptake coefficient parameter. The simulation then divides these total removed nutrients

between any plants with roots in the cell proportionally to their respective masses. This gives,

for instance, a plant with 30% of the root in a cell, 30% of the nutrient taken up, modeling a pure

scramble competition (the simulation allows for independent root uptake efficiencies between

plants to simulate competition between species, but in all model runs presented here, the

competing plants are treated as members of the same species with identical uptake efficiencies).

Nutrients taken up go into the plants' resource pools, from which they build more root mass.

Because the simulation does not include an above-ground component, I use the nutrient levels

remaining in these pools in a given amount of time after the plants have achieved a stable root

structure as a proxy for potential reproductive mass. The structure of the uptake equation

produces a diminishing returns curve with respect to nutrient taken up as root mass in the cell

increases. Nutrient uptake happens across all cells and for all plants simultaneously using matrix manipulations, preventing any first-mover advantage.

After the resource dynamics phase, the model enters the root dynamics phase. Here, each plant tests the marginal gain of adding root to each available cell. A plant may add root to any cell currently containing roots from that plant, or any cell adjacent to a cell containing roots from that plant. Maintenance of existing roots costs the plant resource from its resource pool. While this does allow roots to spread faster in runs of the model featuring functionally larger cells, this has no lasting effect on the shape of the root footprint, and only minimal effect on the nutrient retained for reproduction. The parameters Cf and Cd determine these costs; Cf represents the fixed cost for root maintenance independent of distance from the initial starting cell of the plant, while Cd represents the distance cost of root maintenance, which rises as the distance from the roots of a given cell to the starting cell of the plant rises. While increasing Cd shrinks the diameter of the root footprint, any Cd greater than 0 ensures a hill-shaped root footprint, like those presented in Figure 1.1. Cf has a strong effect on how much root the plant puts into the cells it enters, and Cd determines diameter of the plant's root footprint. The plant repeatedly allocates resource to add root in the accessible cells providing the greatest marginal gain until it has exhausted the resource available for allocation. Given multiple equally profitable choices, plants allocate root randomly between those choices, preventing systematic bias. Also, all plants act simultaneously, preventing any first mover biases.

After the plants have had the opportunity to invest in additional root mass, additional resource enters the landscape in the recharge phase. Resource gained by each cell follows a diminishing returns curve in which those cells with lower current levels of resource gain more resource, approaching a maximum concentration of resource in each cell. This recharge rate can

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either remain constant as the number of plants increases or it can increase proportionally to the number of plants present, depending whether researchers wish to investigate increased competition for nutrients, or increased competition for space, independent of nutrients After the recharge, the time step ends, and the cycle repeats until all time steps have transpired.

Results:

Simulated plants in the model produce a ToC, as predicted, as seen when I compare plants under direct competition (Figure 1.1.a, b, and c) to those separated by a hard barrier (Figure 1.1.d, e, and f). Simulated plants separated by a hard barrier produce less total root mass and more total reproductive mass than the directly competing plants that occupy the same amount of space (Figure 1.2). Separating the plants with a semi-permeable membrane that allows plausible rates of nutrient diffusion across the membrane but prevents roots from directly overlapping prevents the ToC almost as effectively as a hard barrier (Figure 1.1.g, h, and i; Figure 1.2) (See Chapter 3 for an empirical test of this model behavior).

Clonal plants that can pass nutrient between themselves experience no ToC effects, and generate similar root landscapes to those of plants separated by either type of barrier. To simulate this, the one plant consisting of two ramets got two seeds, and shared a common resource pool. The resultant one-plant root footprint is similar to the two-plant root footprints of the hard barrier and membrane treatment levels. (Figure 1.1.j, k, and l – Figure 1.1.j remains blank because the clonal ramet simulation only features one plant; Figure 1.2).

Discussion

A ToC can emerge in situations where the costs and the benefits of a decision get distributed unevenly between decision making agents. In this example, each additional unit of root mass added to the system benefits the plant that produced it, while it reduces the efficiency of the roots of all competing plants. When a plant exploits a nutrient pool in the absence of competition, it balances the costs of roots with the benefits of nutrient uptake, ultimately maximizing its own reproductive capacity. In competitive systems, however, each plant adds root mass past the point of maximum efficiency, because some of the efficiency costs get borne by the other plant. These simulations show that by either physically preventing competition (analogous to the privatization solution to the ToC in human systems), as seen in Figure 1.1.d, e, & f, or by connecting the benefits as well as the costs of growth (analogous to solving the ToC via socialization), as seen in Figure 1.1.k & l, any tragic effects can be avoided.

The model predicts that a semipermeable barrier that allows free flow of nutrients but blocks root growth installed between the growing plants will also mitigate the ToC. In the model, direct root proximity is critical to generating a ToC. A possible biological explanation for behavior in line with this prediction could center on nutrient microenvironment in close proximity to roots. If roots lower nutrient concentration in the immediately adjacent soil or growth medium, but have only a much weaker effect on nutrient concentration further away from root structures (possibly due to relatively low diffusion rates), and if the ToC hinges on strong plant perception of nutrient limitation due to a competitor's roots drawing down nutrient levels in the environment, this result may also be observed in experimental systems. Chapter 3 attempts to test this prediction.

The simulation model presented here suggests several potentially productive lines for future empirical research. Chapter 3 centers on testing the model's prediction that plants separated by a semi-permeable membrane will behave like plants separated by a completely impermeable barrier. Future research should include studies comparing root behavior of connected ramets to that of separate ramets; strawberries represent a potential study species for this effect, as they connect via ramets and generate conspicuous, easily quantified reproductive mass. Developing a better understanding of the ToC has value both for biologists addressing natural systems and for social scientists considering interactions between humans and between human institutions.
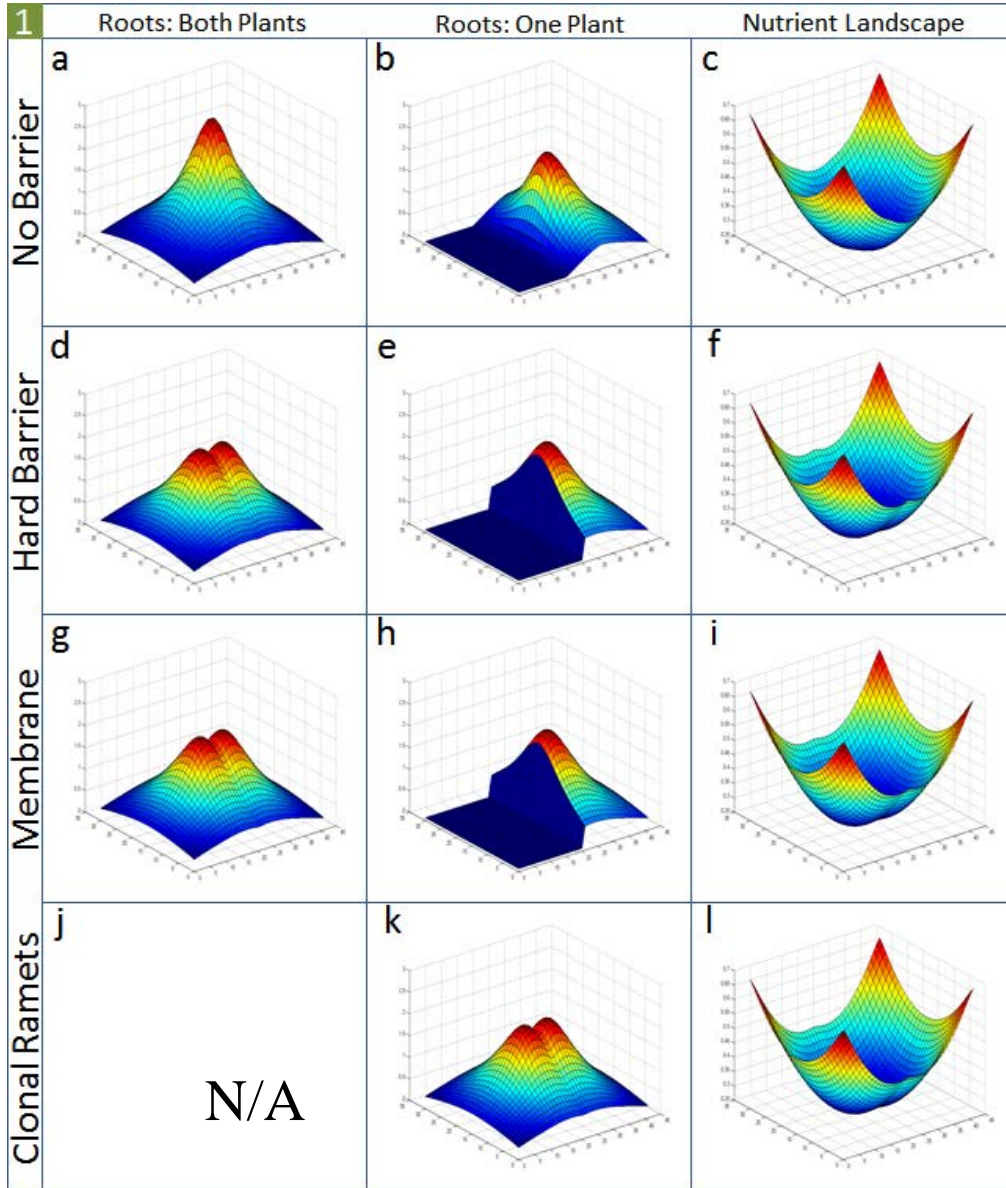
Figure 1.1: Simulated Root & Nutrient Landscapes

Each row of images (e.g.: a, b, and c) displays the results of a single run of the simulation. The first column of images shows the total root mass of both simulated plants, while the second column shows the root mass of one of the two plants, and the final column shows the nutrient landscape at equilibrium. In every case, the x and y axes have units of the x and y coordinates of the spatially explicit simulation, which have an arbitrary magnitude (when the plants represent simulated mosses, each grid square might represent a square millimeter; for simulated oak trees, it might represent a square meter). The z axes of the first two columns mark the amount of root produced, while the z axis of the third column marks the amount of nutrient remaining in the landscape after the root masses have stabilized. The root and nutrient levels all use the same units, which also have an arbitrary magnitude.
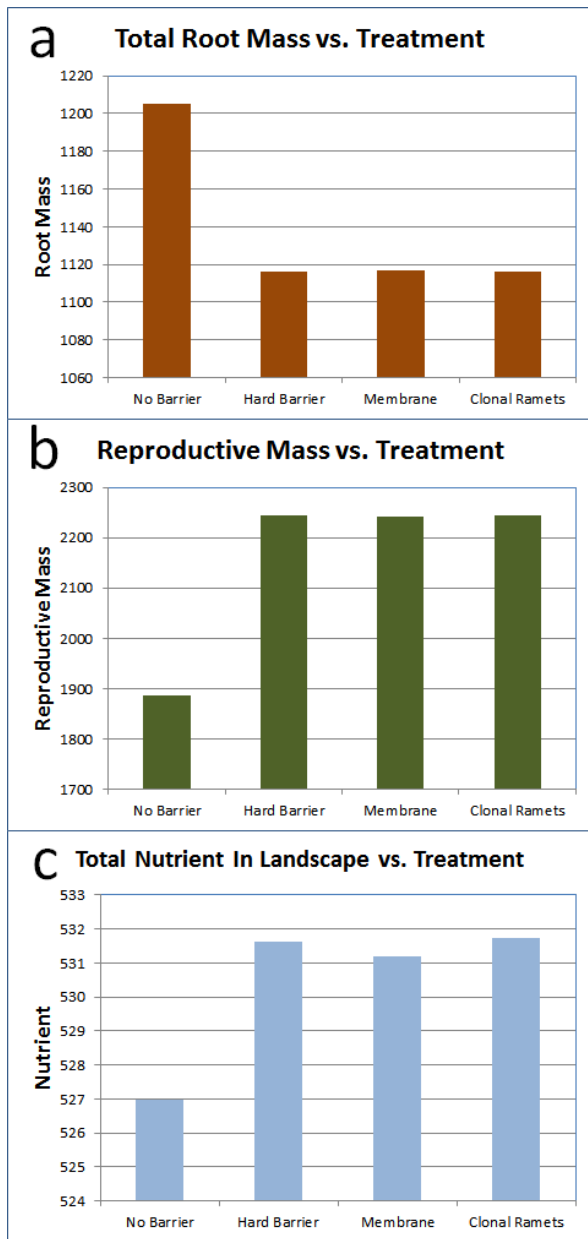
Figure 1.2: Simulated Root Mass, Reproductive Mass, & Nutrient Remaining by Barrier Treatment Level

Total root mass at equilibrium for each of the four treatments. Root mass for the No Barrier simulation differs from the other three simulations, which differ from one another only slightly. I.2.b shows the total reproductive mass produced in each treatment. Again, the No Barrier simulation differs from the other three. I.2.c shows the total nutrient remaining in the landscape at equilibrium. The No Barrier simulation varies widely from the other three; the Membrane simulation varies slightly from the Hard Barrier and Clonal Ramets simulations, which do not vary from one another. As the stochastic portion of the behavior of the model is negligibly small, running traditional statistics on multiple model runs represents pseudoreplication of the data. These graphs therefore present the results of a total of four runs of the model, one under each competition treatment levels, and error bars are not possible.

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Chapter 2 - Nutrient Mediation of Competition in Field Mustard

Introduction

Existing literature (Gersani, et al. 2001; Brown et al., 2005, O'Brien, et al. 2005) suggests that plants grown in a pot with a competitor will produce greater root mass than those grown alone. This root response represents a Tragedy of the Commons (ToC) (Hardin, 1968) in plant root competition, wherein plants in a competitive environment over-allocate resources to root production, leaving decreased resources available for reproductive mass. Subsequent literature (Schenk 2006, Hess & De Kroon, 2007), suggests that the root allocation effect is a response to available rooting space. Schenk sought to replicate the result of Gersani, et al, but failed to generate the same result. Hess & De Kroon studied the effects of spatial limitation and nutrient limitation on individual plants and demonstrated that absolute rooting volume has a significant impact on plant development independent of nutrient availability.

Much existing work indicates that a straightforward ToC framework, in which simply by adding a barrier to divide plants growing together in a pot a researcher could increase plant health and yield, fails to adequately explain critical environmental determinants of plant root behavior. Space availability acts as a significant mediating factor (Schenk 2006, Hess & De Kroon, 2007). Further, access to space can lead to increased reproductive output, even when holding total nutrient amounts constant and, consequently, decreasing nutrient concentration (McConnaughay & Bassas, 1991). Though that trend must reverse for large enough pots.

Previous research into the relationship between nutrient availability and plant interaction indicates that plants grown together in any environment may provide facilitative benefits to one another (Lambers, et al. 1998). Facilitative interactions include volatile release, which can aid in combatting herbivores and infections (Maillette, 1988), and physical support and shading among

shoots. However, competition for limiting resources may hide the effects of facilitation, particularly in stressful environments (Callaway, 1995). Facilitation is highest in low competition, high stress environments (Callaway, et al. 2002), and can come from both sheltering and increased soil nutrient retention (Pugnaire & Luque, 2000). Shading cues, indicative of above-ground competition (Smith, 1995), can decrease allocation to root (Cipollini & Schultz 1999), but even in the presence of shoot shading cues, root competition increases root allocation in relatively high, balanced nutrient environments (Murphy & Dudley, 2007).

I hypothesize that within nutrient treatment levels, I will see a ToC, with higher root mass & root length in open pots, and higher reproductive mass in barrier pots. Consequently, root / shoot ratio should be higher in open pots than barrier pots. I predict that phosphorus limitation will exacerbate the ToC: low phosphorus open pots should fare worse in terms of reproductive mass relative to low phosphorus barrier pots than high phosphorus open pots relative to high phosphorus barrier pots. In terms of root branching, I predict fewer tertiary roots, and, consequently, less branching root structures among low phosphorus pots, in accord with literature for rapid cycling *Brassicas* (Williams, 1986).

Methods

The growth protocol I have developed offers a unique means of studying root behavior *en vivo*, without disturbing the growing plants. Our growth environment consists of 288 100ml beakers. In 144 beakers I installed a hard, biologically inert, watertight, transparent physical barrier that divides the beaker in half, made of cellophane and sealed with silicone adhesive. This barrier both prevents the transmission of nutrients and water between the two sides of the beaker and prevents the roots of plants in barrier beakers from obtaining nutrients from the other

half of the beaker. I placed each beaker into a light barrier consisting of an interior paper layer

and an exterior foil layer to block all light from entering through the sides of the beaker.

Without the light barrier, some seedlings grow down into the gel, rather than up toward the

sunlight.

Each beaker received 70 ml of nutrient gel. The gel consists of a nutrient solution at

either a low phosphorus or a high phosphorus treatment level (see Table 2.1) and gellan gum.

Our recipe modifies Hoagland's Solution (Hershey, 1992, Hoagland & Arnon, 1950) and dilutes

it to roughly $1/10^{th}$ strength. This concentration places nutrient levels low enough that the plants

must compete for nutrients, and high enough that they will still produce seed. The high

phosphorus recipe is standard Hoagland's solution, diluted, while the low phosphorus recipe is a

dilution of Hershey's P- solution. The gellan gum uses the nutrient ions of the Hoagland's

solution to form its gel structure (Grasdalen & Smidsrod, 1987); without these ions it will make a

thick goo solution, but will not set into firm gels. I added 2 mg of $MgSO_4$ per liter of solution as

a gelling agent for additional gel strength. In our final recipe (Table 2.1), the overall $MgSO_4$

level approximates that found in full strength Hoagland's.

I mixed the nutrient solution according to the recipe in Table 2.1, raising the nutrient

solution to 90° C and adding 2.5g of gellan gum powder per liter of solution. I allowed the

mixture to cool to 60°, with vigorous stirring throughout, then poured into the individual beakers.

By covering the beakers in cellophane and refrigerating overnight, I encourage the gel to set.

After the gels set, I cut two semi-circular wells in the gels, directly across from one

another. In barrier pots, I center the wells along the exterior pot wall on each side of the barrier

(see Figure 2.2). The wells run along the side of the beaker down to its bottom. They hold water

(replenished daily throughout the experiment), preventing the gels from drying out and cracking as the plants and evaporative forces remove water from the medium. Further, placing the reservoirs along the sides of the beakers removes the need for standing water on the gel surface, which can both potentially interfere with early seedling development, and encourage algal growth.

Reheating the gels to 90°, either in a microwave or on a hot plate, returns the medium to a liquid state. Plants can then be removed from the gel without damaging the root structure. A straightforward electrical resistance assay using a conductivity tester (eg. the Hanna Instruments Pru mo3 TDS Tester) gives the nutrient concentration remaining in the used, liquified gel.

In each beaker, I measured total root mass, total reproductive mass, and total shoot mass, which I summed to calculate total plant mass. Plants were grown for their full life cycle, of 40 days. I also calculated the root / shoot ratio. I measured the length of the longest root, and calculated the root mass / unit length. After removing the plants from the gels, I measured the gel level remaining in the beaker and the nutrient concentration remaining in the gel.

For each of 61 beakers, I recorded the count of secondary roots (i.e roots that branch directly from the base of the shoot) and of tertiary roots (i.e. roots that branch off of secondary roots). I also calculated the ratio of tertiary to secondary roots, a quantitative measure of branching in root structure. Finally, we measured total plant length, from tip of longest root to tip of longest stem. Again, the transparent gel growth medium specifically affords us the ability to collect these data during plant development without disturbing or damaging the plant.

I analyzed our data using a series of two-way ANOVAs. Ratio measures (total root/total shoot and total root mass/total maximum root length) were first log-transformed to make the data more normal. The resultant p-values are recorded in Table 2.2 (p-values in grey remain

significant after Holm-Bonferroni adjustment for multiple comparisons), and the mean values by treatment level are recorded in Table 2.3 (Holm, 1979). Figure 2.3 presents the root, shoot, reproductive & total plant masses, and Figure 2.4 records the final root mass vs. the final solute concentration by treatment level. Figure 2.1 comprises four photographs of root growth over time of two plants competing for nutrients in the shared root space of an open beaker.

Results

Our results fail to demonstrate any of the hypothesized ToCs, as neither root mass nor reproductive mass varied significantly by barrier treatment level. As such, the interpretation of the data proceeded outside the ToC context. Our root branching data supported our hypotheses, as low phosphorus levels decrease tertiary root production, which consequently decreases root structure branchiness.

The total shoot mass, and total plant mass produced by the two plants in a beaker varied significantly by both nutrient and barrier treatment level (Figure 2.3, b & d), with a significant interaction between the nutrient and barrier treatment levels. Overall, the phosphorus-deprived plants produced significantly less mass than those grown in a full-phosphorus environment. Further, those plants grown in the open (competition) condition produced significantly more mass than those grown separated by a barrier in the full-phosphorus treatment levels, but there was no significant difference in the low phosphorus treatment level.

Reproductive mass and root mass both varied significantly by phosphorus treatment level (Figure 2.3, a & c). Plants grown under phosphorus deprivation produced less reproductive mass and root mass than those grown in a full-phosphorus environment. The mean reproductive mass and the mean root mass produced by plants in the open (competition) treatment level exceeded

that produced by plants in the barrier treatment level in the presence of high phosphorus. Among phosphorus-deprived plants, the reverse was true, but these differences were not statistically significant.

Total plant length (from tip of longest root to tip of longest stem) varied significantly by barrier treatment. Those plants grown in open beakers grew significantly longer than those grown in beakers separated by a barrier.

Root mass per unit root length (a measure of root branching) varied significantly by phosphorus treatment level, but barrier treatment level alone had no significant effect. Plants grown in the high phosphorus environment produced branchier root structures than those grown under depleted phosphorus. The presence of a barrier increased branching among plants grown in a phosphorus depleted environment, but decreased branching among plants grown in a high phosphorus environment.

Root / shoot ratio, nutrient density remaining in the beaker after harvest (a measure of how much nutrient the plants removed from the environment), and gel level remaining after harvest all varied significantly based on phosphorus treatment level, but not on barrier treatment level, and did not show a significant interaction between phosphorus and barrier treatment levels. Plants grown in the low phosphorus nutrient level exhibited a higher root/shoot ratio, and left a higher nutrient concentration behind after harvest (Figure 2.4).

In root branching, the phosphorus treatment levels had a significant effect on both tertiary root count and in the ratio of tertiary to lateral roots (a measure of branching). Plants grown in the depleted phosphorus treatment levels made fewer secondary roots, fewer tertiary roots, and built less branching root structures (fewer tertiary roots per secondary root) than did plants grown in the high phosphorus treatment levels (Figure 2.5). Neither the presence or absence of a

barrier nor the interaction between the barrier and phosphorus treatment levels had any significant effect on secondary root count, tertiary root count, or tertiary to secondary root count ratio.

Discussion

Like a hydroponic system, our protocol system includes the capacity to directly determine the plants' nutrient environment, and to directly view the root structures, to which it adds the physical support to the root structures of a more traditional, solid, growth medium. This physical structure also allows for spatially heterogeneous nutrient distribution in response to root behavior, as the roots deplete nutrients in the immediate vicinity and nutrients difusse down the concentration gradient toward them, as shown in the simulation model in Figure 1.1.

Roots have been shown to discriminate between other roots from the same plant and roots from other plants, and if a plant is divided, its roots treat roots from the other half as foreign to the same extent as the roots of a genetically distinct plant (Gruntman & Novoplanksy, 2004). Gruntman hypothesized (but did not test) that the self-recognition could hinge either on internal hormone (possibly auxin) oscillation or on electrical signaling. To our knowledge, our data represents the first ever demonstration of an environment nutrient-mediated response to the presence of a competitor and additional space, though one previous study (Andalo, et al., 2001) found a similar reversal triggered by CO_2 concentration, rather than environment nutrient availability: Their *Arabidopsis thaliana* grew better in a monogenotypic treatment level at ambient CO_2 levels, and better in a heterogenotypic environment at elevated CO_2 levels. In our full-phosphorus treatment level, access to the whole pot and the presence of a competitor leads to significantly larger plants with a (statistically insignificant) greater reproductive mass. On the

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other hand, in the low phosphorus treatment level, access to the whole pot and its competitor leads to significantly smaller plants with less reproductive mass. The low phosphorus nutrient level also reverses the effect of the barrier treatment levels on the plants in terms of the root/shoot ratio. Among plants in the high phosphorus treatment level, the presence of a barrier leads to more root mass required to maintain a given shoot mass (higher root/shoot ratio), whereas in the low phosphorus treatment level, the presence of a barrier leads to less root mass required to maintain a given shoot mass (lower root/shoot ratio). One study on trembling aspen comparing tree growth with and without competition at both high and low fertilizer treatment levels (Donaldson et al, 2006) found a decrease in plant mass and an increase in root/shoot ratio due to competition in both the high and low fertilizer treatment levels. The data presented here exhibit a nutrient-mediated plant response to the presence of a competitor and additional space. In the low phosphorus treatment level, sharing a complete beaker with a competitor inhibits plant growth and development relative to sole occupancy of a half-beaker. In the high phosphorus treatment level, sharing a complete beaker encourages plant growth and development relative to occupying a half-beaker alone.

Our study of root branching directly utilizes the strengths of our transparent gel growth protocol. By permitting the examination of root structures non-destructively, our gels open opportunities to address new research questions. Our data demonstrate a fundamentally distinct root structure strategy based on nutrient environment. Plants in the high phosphorus treatment level produced significantly more tertiary roots, and consequently maintained significantly ($p < 0.0001$) branchier root structures than those in the low phosphorus treatment level.

Future studies extending these efforts should include the effects of potassium and nitrogen limitation in a full factorial design. An additional treatment level added to the barrier

treatment consisting of a semi-permeable barrier would distinguish between root behavior in response to access to physical space and root behavior in response to nutrient availability and non-self recognition. The semi-permeable barrier would allow nutrients, water, and any water-soluble root exudates to diffuse freely between the two halves of the container, while physically blocking root growth across the barrier. The visibility of roots afforded by the growth protocol makes it possible to track root growth, root branching behavior, and even root hair development across the entire plant life cycle. The key to future studies will lie in leveraging these abilities to maximum effect.

Table 2.1: Nutrient Solution Recipie & Micronutrient Stock Recipie
Table 2.1.a:

Nutrient Solution Recipe:		
Stock Solution	ml stock (complete)	ml stock (no phosphorus)
1M Ca(NO$_3$)$_2$ ● 4H$_2$0	0.5	0.4
1M KNO$_3$	0.5	0.6
1M KH$_2$PO$_4$	0.1	0
1M MgSO$_4$ ● 7H$_2$O	2.2	2.2
0.05M FeNa EDTA	0.1	0.1
Micronutrient Stock	0.1	0.1

Table 2.1.b:

Micronutrient Stock Recipe:	
Micronutrient Salt	g/L
H$_3$BO$_3$	2.86
MnCl$_2$ ● 4H$_2$O	1.81
ZnSO$_4$ ● 7H$_2$O	0.22
CuSO$_4$ ● 5H$_2$O	0.08
H$_2$MoO$_4$ ● H$_2$O	0.02

Table 2.1.a: The recipe for each of our two nutrient treatment level gels. They represent dilution of recipes from Hershey, 1992, and Hoagland & Arnon, 1950, respectively. Table 2.1.b: The recipe for the micronutrient stock solution.

Table 2.2: 2-Way ANOVA p-values:

Raw Numbers (except LNs)	barrier	nutrient	interaction
total root mass	0.0434	< 0.0001	0.0015
total reproductive mass	0.2728	< 0.0001	0.2586
total shoot mass	0.0001	< 0.0001	< 0.0001
total mass	0.0014	< 0.0001	< 0.0001
Log (root mass / shoot mass)	0.9378	< 0.0001	0.0667
total length	0.0005	0.6172	0.9268
log (root mass per length)	0.1084	<0.0001	0.0058
mean nutrient concentration	0.7859	< 0.0001	0.1916
gel level	0.0782	0.0037	0.0678
Branching Study:			
lateral root count	0.4533	0.011	0.7109
tertiary root count	0.6183	< 0.0001	0.8704
branchiness (log (tert/lat))	0.4642	< 0.0001	0.6593

Table 2.2: p-values from 2-Way ANOVAs – The shaded values are significant at an alpha of 0.05 after applying the Holm-Bonferroni method to account for multiple comparisons. Barrier represents the effect of the barrier treatment levels on the listed response variable, nutrient represents the effect of the nutrient treatment levels on on the listed response variables, and interaction represents the strength of the interaction between the two.

Table 2.3: Means & Standard Errors

	Barrier	Open
Total Root (mg) High P	6.1 ± 0.3	7.3 ± 0.2
Total Root (mg) Low P	4.3 ± 0.2	4.0 ± 0.2
Total Repro (mg) High P	11.5 ± 0.7	12.8 ± 0.8
Total Repro (mg) Low P	1.3 ± 0.2	1.3 ± 0.2
Total Shoot (mg) High P	22.0 ± 0.8	28.6 ± 0.9
Total Shoot (mg) Low P	10.0 ± 0.5	9.0 ± 0.5
Total Mass (mg) High P	39.7 ± 1.4	48.7 ± 1.5
Total Mass (mg) Low P	15.6 ± 0.8	14.3 ± 0.8
Root / Shoot High P	0.284 ± 0.01	0.265 ± 0.01
Root / Shoot Low P	0.452 ± 0.02	0.500 ± 0.03
Total Length (cm) High P	14.8 ± 0.6	16.9 ± 0.6
Total Length (cm) Low P	14.4 ± 0.6	16.6 ± 0.7
Root Mass / Length (mg/mm) High P	0.427 ± 0.02	0.456 ± 0.02
Root Mass / Length (mg/mm) Low P	0.306 ± 0.02	0.246 ± 0.01
Nutrient Left (ppm) High P	361.6 ± 5.1	367.4 ± 3.9
Nutrient Left (ppm) Low P	473.4 ± 5.5	464.6 ± 7.3
Gel Remaining (ml) High P	50.2 ± 1.4	54.0 ± 0.8
Gel Remaining (ml) Low P	55.2 ± 1.1	55.1 ± 0.7

Branching Study

	Barrier	Open
Lateral Roots High P	13.3 ± 1.1	12.9 ± 0.8
Lateral Roots Low P	11.1 ± 1.1	10.0 ± 0.8
Branching (ln(tert / lat)) High P	0.494 ± 0.1	0.556 ± 0.2
Branching (ln(tert / lat)) Low P	-0.603 ± 0.4	-0.351 ± 0.2
Tertiary Roots High P	22.8 ± 2.8	24.4 ± 2.6
Tertiary Roots Low P	8.3 ± 2.0	9.1 ± 1.8

Table 2.3: The means (with standard errors) of each of the response variables, by barrier and phosphorus treatment levels. In each case a grey background denotes the larger mean value between the two barrier treatment levels.
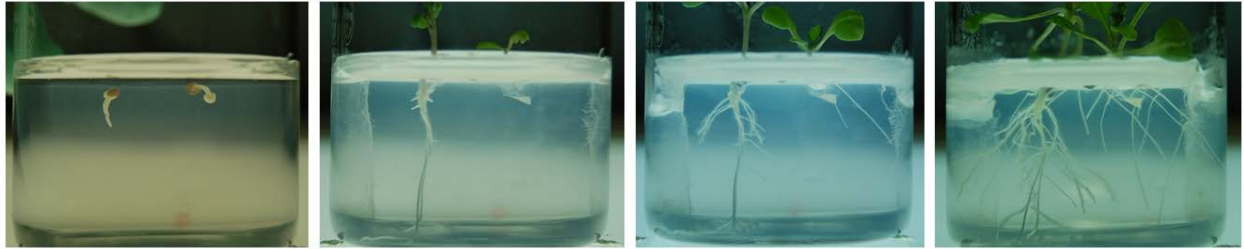
Figure 2.1: Root Growth Over Time With Competition

Two plants grown in an open beaker, with photographs taken across the first few weeks of root development.

Figure 2.2: Bottom-Up View of a Barrier Pot with Growing Plant Roots & Visible Wells
          Two plants grown in a barrier pot, seen from beneath the beaker. Note the watering wells
at the far left and far right of the beaker.
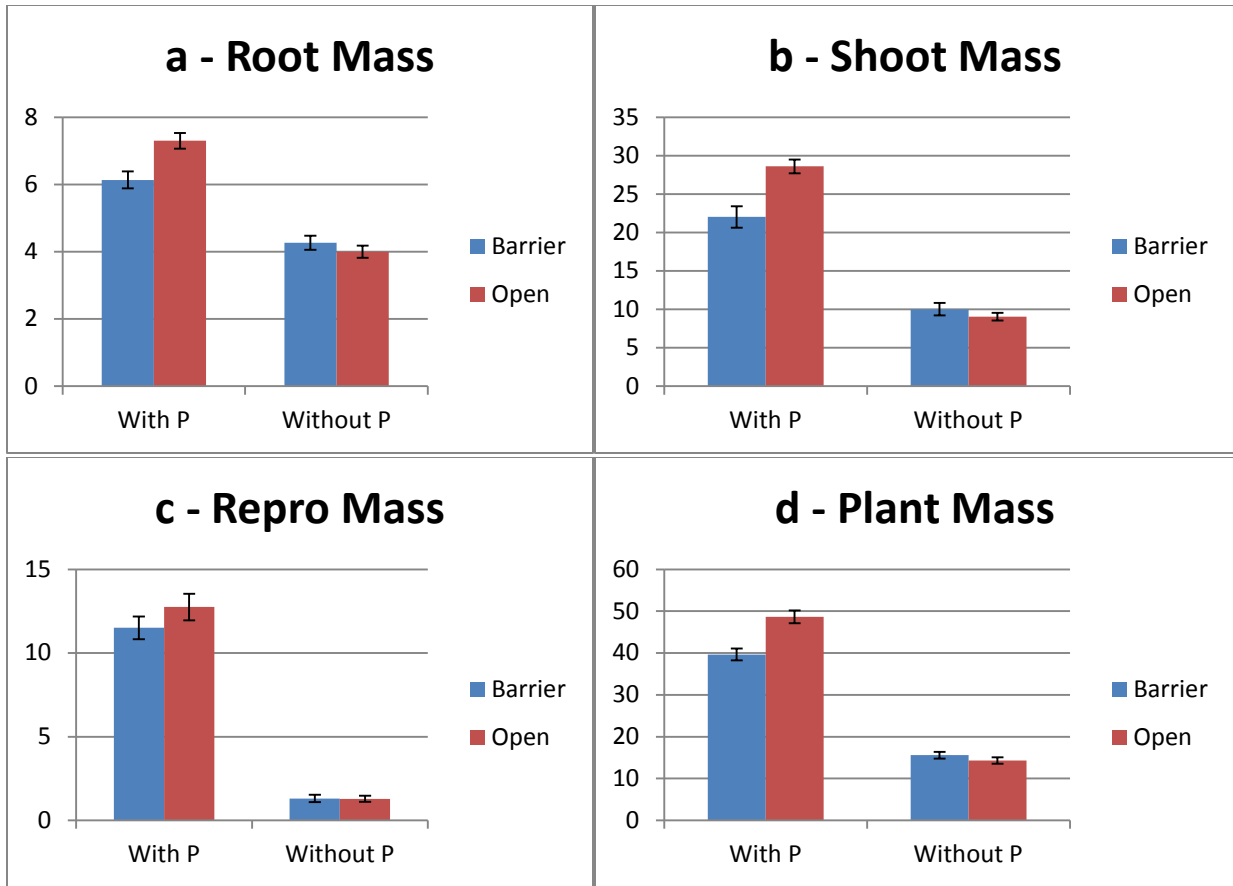
Figure 2.3: Root, Shoot, Reproductive, and Total Masses

Graphs the root (a), shoot (b), reproductive (c), and total plant (d) masses, with standard error bars. All measures are in milligrams.
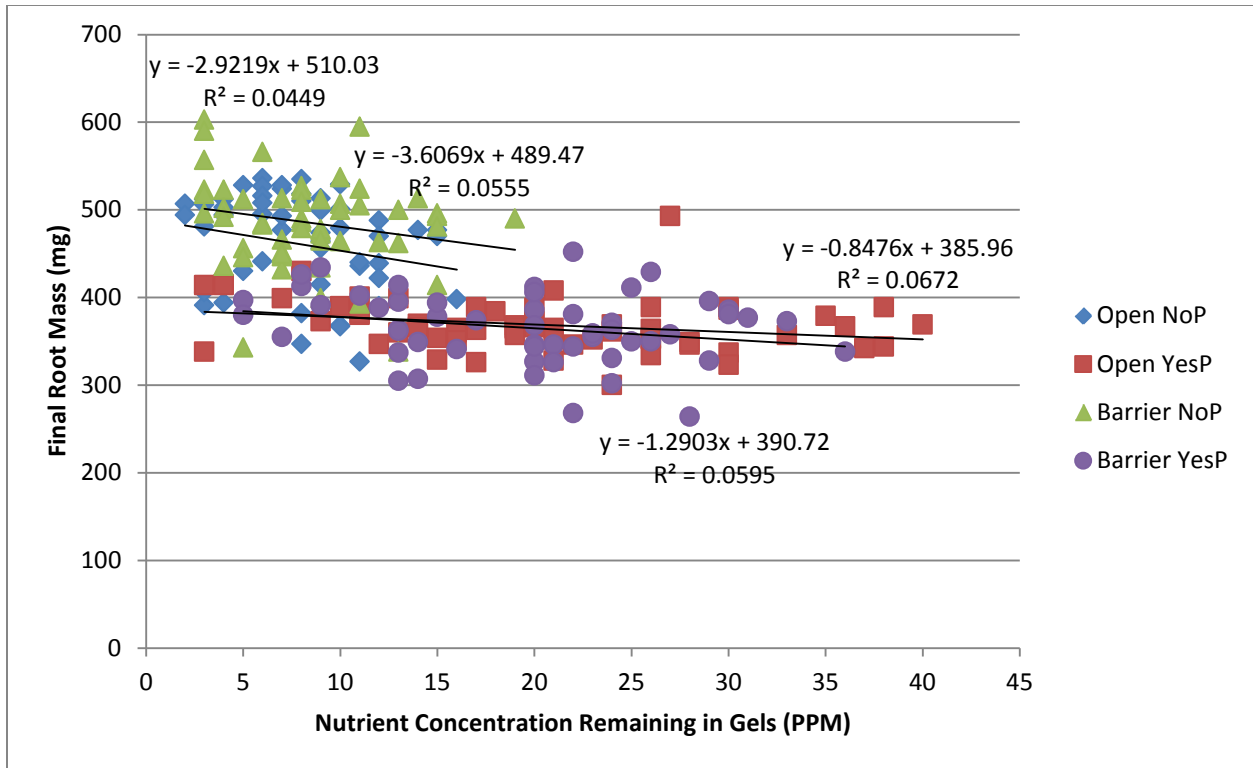
Figure 2.4: Final Root Mass vs. Final Solute Concentration by Treatment Level

Concentration of solutes remaining in the beakers after harvest (in PPM) against final root mass (in mg) by barrier and nutrient treatment levels. The plants in the low phosphorus treatment levels, barrier (green triangles) and open (blue diamonds), being smaller, leave more nutrient behind in the gels per unit root mass than do the larger plants in the full phosphorus treatment levels, barrier (purple circles) and open (red squares).
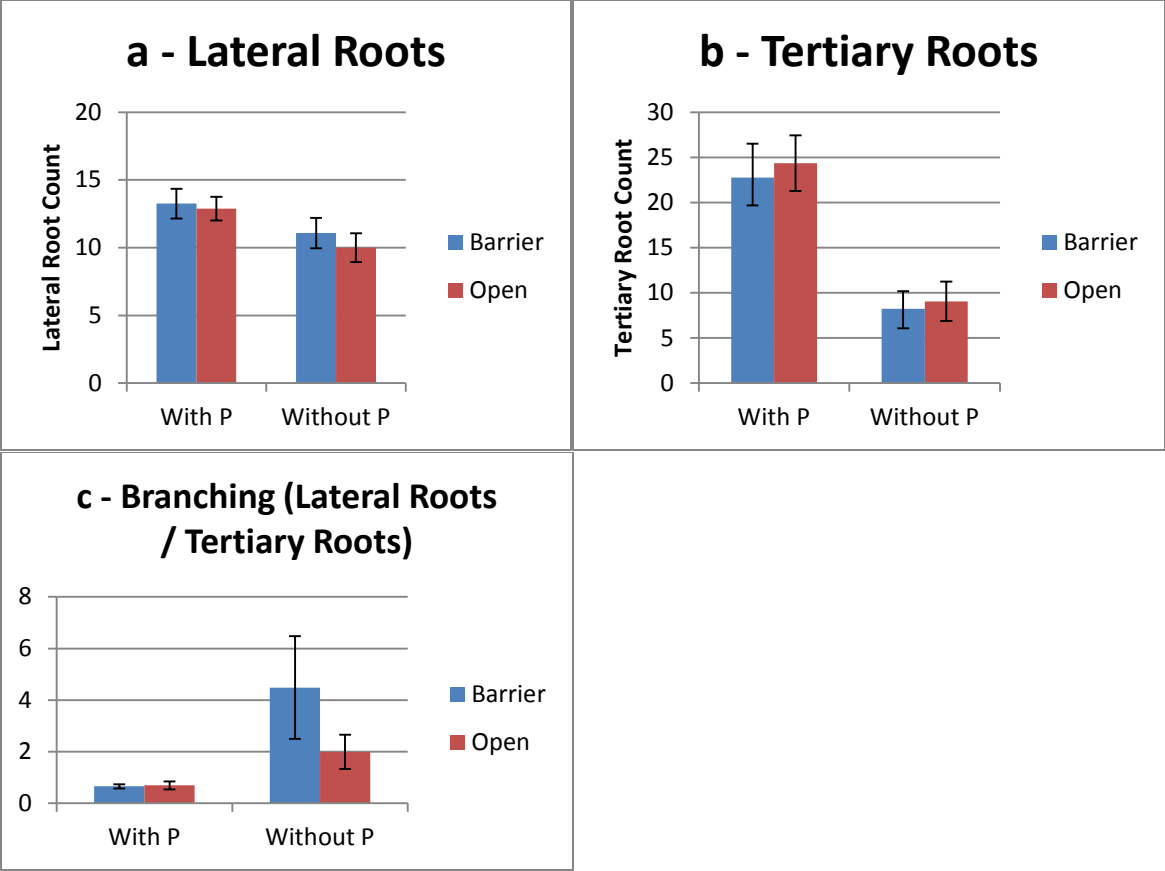
Figure 2.5: Branching Results
Root branching parameters by nutrient and barrier treatment levels. Units in 2.5.a & 2.5.b are root counts, while the ratio units of 2.5.c are unitless.

Chapter 3 – The Semi-Permeable Membrane

Introduction

Existing research (Gersani, 2001) suggests that plant root competition can give rise to a Tragedy of the Commons (ToC) in which plants under root competition for nutrients over-allocate resources to roots, ultimately rendering them less able to generate reproductive structures. Further, this effect should exist regardless of whether the plants can sense each other's presence in any way other than by detecting local nutrient availability. Subsequent work (Schenk 2006, Hess & De Kroon, 2007) suggests that the physical size and shape of the rooting space has a greater effect on plant success than does the presence or absence of a competitor. Several open questions in this field center on the sources of ToC plant behavior. Are they triggered by the plants' awareness of competitor's root exudates? Are they strictly nutrient mediated? What environmental factors would aggravate (or, conversely, alleviate) the effect? Our own simulation model (presented in Chapter 1) suggests both that close root proximity between competitors is necessary for a ToC, and that no knowledge of the other plant beyond perception of local nutrient availability is required.

In order to empirically test these model results, I constructed growth beakers in three treatment levels. Open beakers lacked any separating barrier between the plants. Hard barrier beakers featured a water-tight divider between the plants preventing any root competition. And beakers in the semi-permeable treatment level featured a fine-pored filter membrane barrier that prevents root growth between the two halves of the beaker but permits the diffusion of nutrients, water, and any water-soluble root exudates between the halves. If detection of the second plant triggered the ToC, I should have observed plants in the semi-permeable membrane treatment level behaving like those in the open treatment level. If, on the other hand, nutrient micro-

environment effects of close root proximity gave rise to the ToC, or if available plant rooting space drove root behavior, I should observe plants in the semi-permeable membrane treatment level behaving like those in the hard barrier treatment level. Presumably, if nutrient micro-environment is the critical factor, systems with higher nutrient diffusion rates would allow for the effect to occur at greater distances between roots.

I predicted that, in accord with existing literature, the plants' behavior in the Open treatment level would lead to a tragedy of the commons (ToC). By over-allocating resources to root development relative to those in the Barrier treatment, I predicted that plants in the open treatment would produce greater root mass, and, ultimately, as a result of this over-allocation, produce less reproductive mass than plants grown in either of the two barrier treatment levels. In accord with our existing computer models (Chapter 1; Miller & Crowley 2011), I predicted that the plants in the Membrane treatment would behave similarly to those in the barrier treatment (see Figure 3.1).

Methods

I planted 512 Wisconsin Fast Plants (*Brassica rapa*) from seed in 256 100ml beakers (2 plants per beaker) in the greenhouse, each containing 60 ml of transparent gellan/Hoagland's solution substrate. Each beaker came from one of three treatment levels, Open (no barrier), Barrier (featuring a hard plastic barrier that divides the beaker into two independent, water-tight halves), and Membrane (featuring a semi-permeable membrane that divides the beaker in half, blocking root growth, but permitting nutrient diffusion between the halves). The membrane is an industrial filter made of woven silk featuring a pore size large enough to allow free passage of water and nutrients. Each treatment level included roughly 1/3 of the total beakers. Plants were

allowed to live out their full life cycle, and were harvested after seed production, at 42 days.

Table 1.1 reports the results of the study. Each p-value comes from a one-way ANOVA, and the

independent variable in each test was the beaker barrier type.

Results

Total within-pot shoot mass varied significantly (p = 0.0060) by barrier type, with plants

grown in open pots having more shoot mass (68.7 mg +/- 1.9) than those grown in pots with a

hard (61.2 +/- 1.7) or semi-permeable (62.7 +/- 1.6) barriers (which do not differ

significantly from one another). Post-hoc independent t-tests showed that total pot shoot mass

differs between open and hard barrier treatment levels (p = 0.0038), and between open and semi-

permeable barrier treatment levels (p = 0.0169), but not between hard and semipermeable barrier

treatment levels (p = 0.5279). These differences became even more distinct when only looking

at the heavier of the two plants in the pot. Here, those grown in an open pot have more shoot

mass (46.6 mg +/- 1.4) than those grown in pots with a hard (36.0 mg +/- 1.0) or semi-permeable

(38.2 mg +/- 1.2) barriers (which do not differ significantly from one another). Post-hoc

independent t-tests show that shoot mass of the heavier plant differs between open and hard

barrier treatment levels (p < 0.0001), and between open and semi-permeable barrier treatment

levels (p = 0.0091), but not between hard and semipermeable barrier treatment levels (p =

0.1697).

Neither root mass nor reproductive mass significantly varied by barrier type. But I did

see a significant effect of barrier type on shoot mass. The barrier only extends a couple of

millimeters above the gel substrate in each beaker, so I believe that its direct effect on above-

ground competition must be negligible, but indirectly, through the roots, the presence or absence

of a root barrier significantly affects shoot growth, with plants grown in open beakers producing over 10% more shoot mass than those grown in beakers with hard barriers ($p = 0.0060$). Plants grown under the membrane treatment grew an intermediate amount of shoot mass not significantly different from the shoot mass of plants grown in beakers with hard barriers. When I look only at the smaller of the two plants in each beaker, the effect disappears completely ($p = 0.5687$). When I look only at the larger of the two plants in each beaker, the effect becomes much more pronounced, with mean open beaker mass at over 20% more than mean barrier beaker mass ($p < 0.0002$). Also, the ratio of the shoot mass of the bigger plant in each beaker to its cohabitant smaller plant varies significantly by barrier type ($p = 0.047$) with the mean ratio in open beakers exceeding the mean ratio in barrier beakers by roughly 60%. Both these p-values remain significant at an alpha of 0.05 after correcting for multiple comparisons using the Holm-Bonferroni adjustment (Holm, 1979).

Discussion

Our data fails to demonstrate the presence of a root competition mediated commons tragedy in this system, as neither reproductive structure production nor root production varies significantly by treatment level. As such, any inferences from these data to the causes of the Tragedy of the Commons in plant root competition would be substantively speculative. Our significant results run directly contrary to our predictions. I predicted that, in line with previous research (Gersani, 2001), plants would benefit from root isolation in our barrier treatments levels. But plants in the open treatment level grew approximately 10% more shoot mass than those in the barrier treatment levels.

Comparison of only the smaller of the two plants in each beaker yields no significant results whatsoever, while comparison of only the larger of the two plants yields more significant results (p = 0.0002) on shoot mass than comparisons of total pot shoot mass (p = 0.006). This indicates that the larger plants' shoot mass differences drive the total plant shoot mass difference. Of the plants in the study, those that win the root competition in the open beakers get the best access to substrate nutrients. I do not currently understand why they then allocate these resources to shoot mass, and, specifically, not to reproductive mass.

One possible explanation for these results hinges on within pot plant asymmetry. When seeds germinate at different rates, one seed in each pot gains first access to the pot's nutrient supply. In cases where the two plants are separated by a barrier (either hard or semi-permeable), that barrier helps defend the slower, smaller plant from root competition from the faster, larger plant. In our membrane pots, shoot masses take an intermediate value between those of the hard barrier and open pot treatment levels, both for pot total shoot mass and for the mass of only the heavier plant. This suggests that the bigger plant successfully pulls nutrient from the smaller competitor's half of the pot in membrane pots.

Pilot data indicates that *Brassica rapa* would grow more massive if grown in gels of higher nutrient concentration than those used in this experiment, indicating nutrient limitation at these levels. Future studies should address the relationship between nutrient levels and the competition effects observed by featuring high and low nutrient treatment levels across all three barrier type treatment levels, using the nutrient concentration of this study as the high nutrient treatment level.

Table 3.1: ANOVA p-values, With Means & Standard Errors

ANOVA vs. Barrier	p-value	Barrier Mean	Membrane Mean	Open Mean
Pot Total Root Mass	0.6292	11.7 mg ± 0.4	12.3 mg ± 0.5	12.2 mg ± 0.4
Pot Total Repro Mass	0.1463	29.3 mg ± 1.6	32.9 mg ± 1.4	32.8 mg ± 1.4
Pot Total Shoot Mass	**0.0060**	**61.2 mg ± 1.7**	**62.7 mg ± 1.6**	**68.7 mg ± 1.9**
Root/Shoot Ratio	0.0695	0.19 ± 0.01	0.19 ± 0.1	0.18 ± 0.01
Bigger Plant's Root Mass	0.5212	7.1 mg ± 0.2	7.5 mg ± 0.4	7.5 mg ± 0.3
Bigger Plant's Repro Mass	0.0586	19.3 mg ± 1.0	22.7 ± 1.2	22.2 mg ± 1.02
Bigger Plant's Shoot Mass	**0.0002**	**36.0 mg ± 1.0**	**38.2 mg ± 1.2**	**46.6 mg ± 1.4**
Smaller Plant's Root Mass	0.8911	4.6 mg ± 0.3	4.8 mg ± 0.2	4.7 mg ± 0.2
Smaller Plant's Repro Mass	0.8488	10.0 mg ± 0.8	10.2 mg ± 0.7	10.6 mg ± 0.7
Smaller Plant's Shoot Mass	0.7288	25.3 mg ± 1.0	24.5 mg ± 1.0	25.6 mg ± 1.1

Table 3.1: p-values from 1-Way ANOVAs, with means & standard errors – The values in bold are significant at an alpha of 0.05 after applying the Holm-Bonferroni method to account for multiple comparisons, which did not change which values are significant.
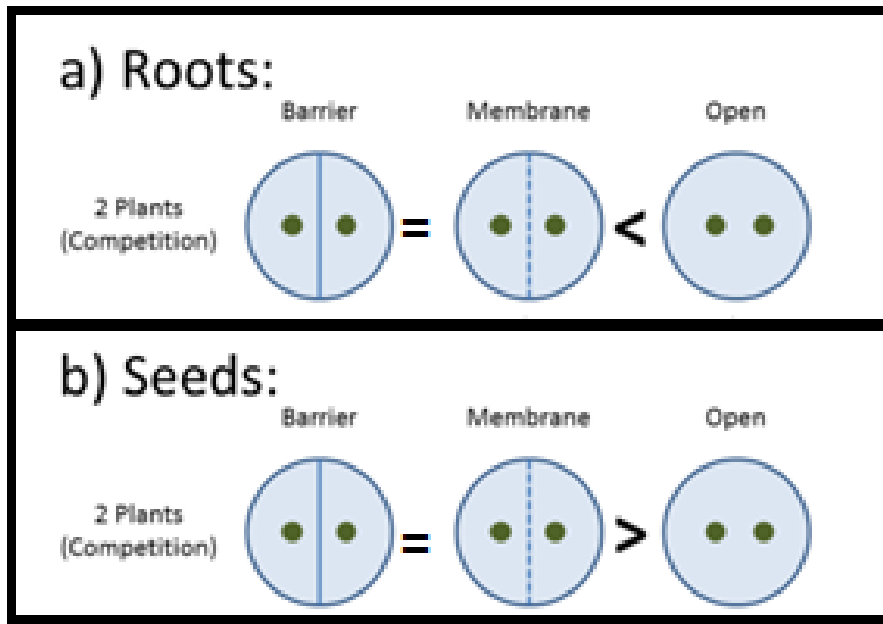
Figure 3.1 – Predictions Roots & Reproductive Mass:

I predicted, based on the computer simulation presented in Chapter 1, that plants grown in open pots would produce more roots and less reproductive mass than plants grown in either the barrier or the membrane treatment levels, and that the barrier and membrane treatment levels would show no significant difference in the production of root or reproductive mass. Biologically, this prediction represents the case where close root proximity between competitors and the resultant particularly low levels of nutrient in the microenvironment directly around the roots triggers the ToC.

a - Root Mass (mg)

b - Shoot Mass (mg)

c - Reproductive Mass (mg)

d - Root / Shoot Ratio

e - Heavier Plant's Shoot Mass (mg)
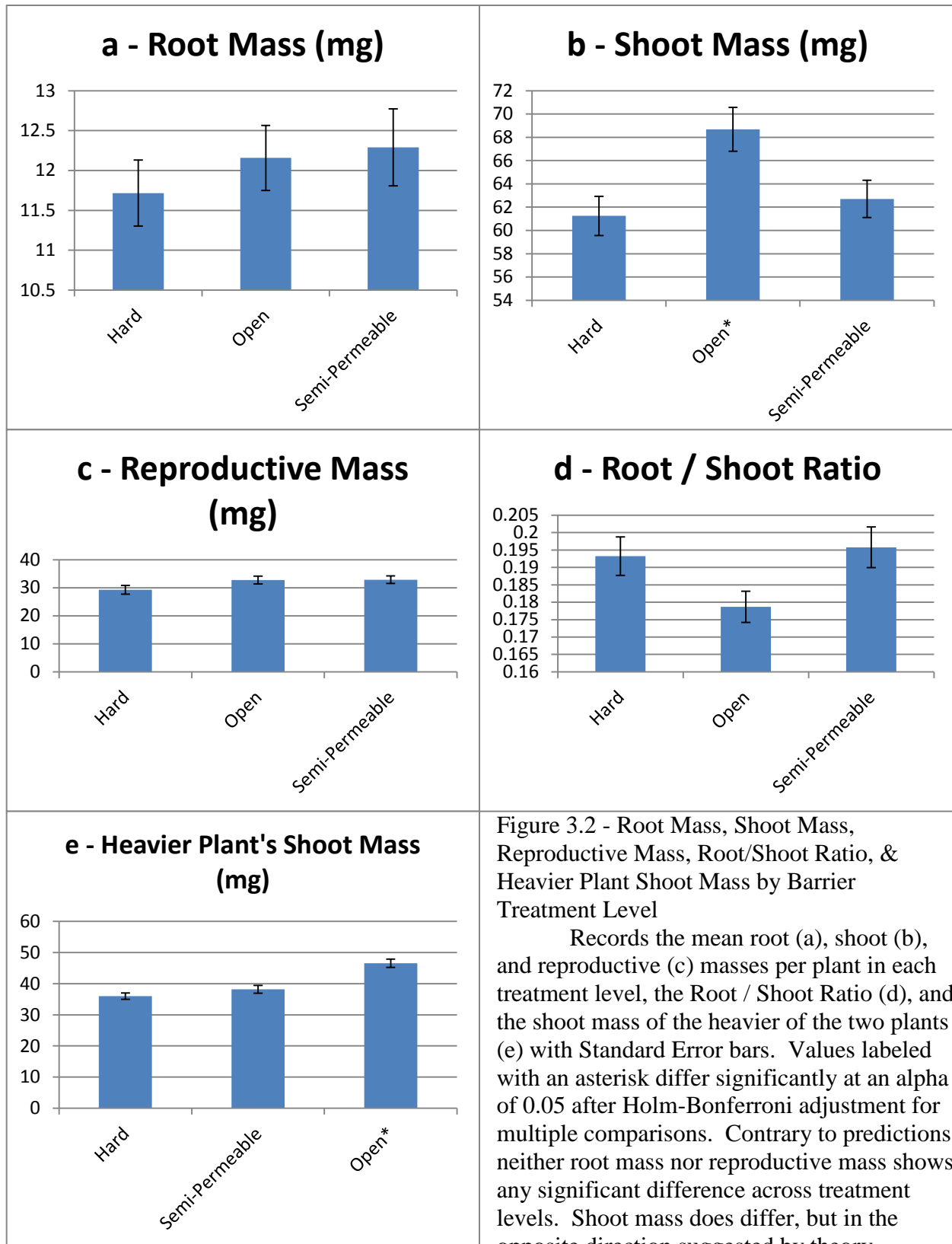
Figure 3.2 - Root Mass, Shoot Mass, Reproductive Mass, Root/Shoot Ratio, & Heavier Plant Shoot Mass by Barrier Treatment Level

Records the mean root (a), shoot (b), and reproductive (c) masses per plant in each treatment level, the Root / Shoot Ratio (d), and the shoot mass of the heavier of the two plants (e) with Standard Error bars. Values labeled with an asterisk differ significantly at an alpha of 0.05 after Holm-Bonferroni adjustment for multiple comparisons. Contrary to predictions, neither root mass nor reproductive mass shows any significant difference across treatment levels. Shoot mass does differ, but in the opposite direction suggested by theory.

1. SimRoots.m

```
%SimRoots.m - Main simulation program - RUN THIS PROGRAM FROM THE
COMMAND LINE %includes parameter initialization, the main program
loop, and data recording

clear

%Get rid of Excel output file from any previous set of runs in
preparation for coming data (REMEMBER TO RENAME sandy.xls BEFORE
STARTING A NEW SET OF RUNS IF YOU WANT TO KEEP THE DATA).

delete sandy.xls

%variables to record between runs
%total root mass in the landscape
rootsumx = [];
%total nutrient remaining in the landscape
nutsumx = [];

%total resource kept in the plants' resource pools (a proxy for
reproductive production)
poolx = [];
poolsumx = [];

r1 = {'rootsum'};
n = {'nutsum'};
p2 = {'poolsum'};

%prepping for Excel format output after the run
Ax = 'A%d';
Bx = 'B%d';
Cx = 'C%d';
Dx = 'D%d';
Ex = 'E%d';
Fx = 'F%d';
Gx = 'G%d';
Hx = 'H%d';
Ix = 'I%d';
Jx = 'J%d';
Kx = 'K%d';
Lx = 'L%d';
Mx = 'M%d';
Nx = 'N%d';
```

```
Ox = 'O%d';

%for multiple sequential runs of the model, the number of total runs
emcee = 2;

for master = 1:emcee
    %parameters for the run (the comments include suggested formulae
    for adjusting the parameter across multiple runs to analyse the
    effect of the parameter on plant behavior):
    dmaster = 1;
    %(round(mod((master+5),12)/12)*58)+2;
    %number of diffusion cycles per root cycle

    plantcount = 1;
    %2-(round(mod((master+2)+1,2)/2)*1);
    %number of plants

    ymax = 3;
    %14-(round(mod((master+2)+1,2)/2)*7);
    %landscape size in y-dimension

    xmax = 3;
    %landscape size in x-dimension

    maxtime = 500;
    %simulation duration in timesteps

    memb = 0;
    %-(round(mod((master+0),3)/3)*-2.5);
    %semi-permeable membrane position (0 for no membrane)

    psych = 0;
    %round(mod((master+11),24)/24);
    %psychic plants setting - Boolean - Can the plants see one
    timestep into the future when making their root allocation
    decisions?

    d = 0;
    %.146;
    %(round(mod((master+5),12)/12)*.14)+.003;
    %diffusion - NEVER set to over .146 (can cause negative resource
    values)

    fcst = 0.00001;
    %fixed cost of root maintenance
```

```
gamma = 0;
%.005;%round(mod((master+2),6)/6)*.0005;
%(round(mod((master+2),6)/6)*.005); %distance cost of root
maintenance

fract = 1;
%power of increasing distance costs

smell = 1;
%round(mod((master+11),24)/24);
%Self/NonSelf Awareness - Boolean - do the plants have an
awareness of each other, separate from via awareness of change in
nutrient levels in the cell?

xstart = [2 2]; %The starting x-values for the plants' seeds
ystart = [2 2]; %The starting y-values for the plants' seeds

qr = .001/master;
%size of a quantum of root mass, the smallest amount of root a
plant can allocate, in units of resource

w = .025/master;
%*(floor(mod(4,master)/4))+.0001;  %resource recharge rate, the
rate at which "nutrient rain" restores the nutrients in the
landscape;

k = 2/master;
%2/((1+(master*2))^2); %4.5*(round(mod(master+1,4)/4))+.5;
%max concentration, the maximum nutrient level a cell of the
landscape can hold; full landscape cell nutrient saturation level

u = .1; %plant uptake rate
r = 2/master; %4/((1+(master*2))^2); %10/((1+(master*2))^2); %
direct additive recharge
pool = [];

%Give each plant its initial resource pool
for andy = 1:plantcount
    pool = [pool .01/master];
    %determines the size each "seed" - To study the effect of
    seed size heterogeneity, assign each seed value individually
    rather than in this loop.
end
```

```matlab
%prepping for Excel format variable recording
xAx = sprintf(Ax,master);
xBx = sprintf(Bx,master);
xCx = sprintf(Cx,master);
xDx = sprintf(Dx,master);
xEx = sprintf(Ex,master);
xFx = sprintf(Fx,master);
xGx = sprintf(Gx,master);
xHx = sprintf(Hx,master);
xIx = sprintf(Ix,master);
xJx = sprintf(Jx,master);
xNx = sprintf(Nx,master);

%Record parameter values from the run into excel
xlswrite('sandy.xls',plantcount, 'Sheet1', xAx)
xlswrite('sandy.xls',xmax, 'Sheet1', xBx)
xlswrite('sandy.xls',ymax, 'Sheet1', xCx)
xlswrite('sandy.xls',xstart, 'Sheet1', xDx)
xlswrite('sandy.xls',ystart, 'Sheet1', xEx)
xlswrite('sandy.xls',memb, 'Sheet1', xFx)
xlswrite('sandy.xls',psych, 'Sheet1', xGx)
xlswrite('sandy.xls',dmaster, 'Sheet1', xHx)
xlswrite('sandy.xls',d, 'Sheet1', xIx)
xlswrite('sandy.xls',gamma, 'Sheet1', xJx)
xlswrite('sandy.xls',master, 'Sheet1', xNx)

pool_his = [];
%Generate the initial nutrient landscape and plant the seeds
[resland, distmat, membmat] =
matgen(xmax,ymax,xstart,ystart,plantcount,memb, fract,k);
resland
roots1 = 0;


for timecount = 1:maxtime %main loop
    %nutrient diffusion step
    [resland] = diffuse(resland,dmaster,xmax,ymax,d);
    %resource dynamics step (plants take up nutriend from the
landscape)
    [resland, profit] = resdyn(resland, xmax, ymax, plantcount,
    u, fcst, gamma, distmat);
    pool = pool + profit;  %add nutrient uptake to plant
resource pools
```

```
        %root dynamics (plants allocate resource to roots, as
desired)
        [resland, pool] =
        rootdyn(u,qr,pool,resland,fcst,gamma,xmax,ymax,plantcount,di
        stmat,dmaster,d,psych,membmat,smell);

        % add the recharge
        resland(:,:,1) = resland(:,:,1) + (w*((k-
resland(:,:,1))/k));

        %updates the within-run root history array to include total
        root mass of plant 1
        roots1 = [roots1 sum(sum(resland(:,:,2)))];

        %updates the within-run nutrient pool history array to
        include current resource pool of plant 1
        pool_his = [pool_his pool(1)];

        %outputs finished timestep number to screen for monitoring
progress
        timecount
    end

    finalprofit = pool_his(maxtime) - pool_his(maxtime-1);
    rootsum = 0;
        for inc = 1:plantcount
            %find total root mass across all cells and all plants
            rootsum = rootsum + sum(sum(resland(:,:,inc+1)));
        end
    %update the across-run root sum history array to include the
    final total root sum of this run
    rootsumx = [rootsumx rootsum];
    %updates the across-run nutrient sum history array to include the
    final total nutrient remaining in the landscape after this run
    nutsumx = [nutsumx sum(sum(resland(:,:,1)))];
    %updates the across-run remaining pool (reproduction) history
    array to include the final (reproduction) of this run - includes
    separate value for each plant for each run
    poolx = [poolx pool];
    %updates the across-run remaining pool (reproduction) history
    array to include the final total (reproduction) of this run -
    sums the values for each plant for each run
    poolsumx = [poolsumx sum(pool)];
    tmp = zeros(xmax,ymax);
    for inc = 1:plantcount
```

```
        tmp = tmp + resland(:,:,1+inc);
    end

    %allows recording of each plant separately, below
    offset = (master * 5) - 3;
    %prep target locations in excel sheet for writing, below
    first = sprintf(Ax,offset);
    second = sprintf(Ax,offset+1);
    third = sprintf(Ax,offset+2);
    fourth = sprintf(Kx,master);
    fifth = sprintf(Lx,master);
    sixth = sprintf(Mx,master);
    seventh = sprintf(Ox,master);
    eighth = sprintf(Cx,offset+1);
    ninth = sprintf(Cx,offset+2);

    %write results of model run to excel sheet
    xlswrite('sandy.xls',r1, 'Sheet1', first)
    xlswrite('sandy.xls',n, 'Sheet1', second)
    xlswrite('sandy.xls',p2, 'Sheet1', third)
    xlswrite('sandy.xls',rootsum, 'Sheet1', fourth)
    xlswrite('sandy.xls',sum(sum(resland(:,:,1))), 'Sheet1', fifth)
    xlswrite('sandy.xls',sum(pool), 'Sheet1', sixth)
    xlswrite('sandy.xls',finalprofit, 'Sheet1', seventh)
    xlswrite('sandy.xls',sum(sum(resland(:,:,1)))*2, 'Sheet1',
eighth)
    xlswrite('sandy.xls',sum(pool)*2, 'Sheet1', ninth)

    resland
    %output run # to screen as each run finishes
    master
    figure
    %output image of resource landscape
    surf(resland(:,:,1))
    figure
    %output image of Plant 1's root mass allocation
    surf(resland(:,:,2))
end
```

```
%matgen.m Generates the initial resource landscape matrix, including
placing the semipermeable membrane (if present) and planting all seeds

function[resland, distmat, membmat] = matgen(xmax, ymax, xstart,
ystart, plantcount,memb,fract,k)

    %Layers:
    %1 - Current Resource Concentration
    %2 - Root Concentration: Plant #1
    %3 - Root Concentration: Plant #2
    %and further layers for additional plants, as necessary

    %build landscape:
    membmat = ones(xmax,ymax,plantcount);
    resland = ones(xmax, ymax);
    resland = resland .* k;
    distmat = zeros(xmax,ymax);

    %plant seeds
    for andy = 1:plantcount
        resland(:,:,(1+andy)) = zeros(xmax,ymax);
        resland(xstart(andy),ystart(andy),1+andy) = .01;
    end

    %build a distance matrix from the center of each plant (where the
    seed got planted) to every cell in the landscape - speeds up root
    calculations later to do this once here, rather than every time
    we want to know how far a cell is from the plant later
    for andy = 1:plantcount
        for billy = 1:xmax
            for carly = 1:ymax
                distmat(billy,carly,andy) = (abs(billy-
                xstart(andy))^2 + abs(carly-ystart(andy))^2)^.5;
            end
        end
    end

    %allow distance costs to scale by a power of distance, if desired
    distmat = distmat.^fract;
    distmat = distmat + 1;

    %install semi-permeable membrane, if present
    for andy = 1:plantcount
```

```
        for billy = 1:xmax
            for carly = 1:ymax
                if (memb > 0) && ((ystart(andy) > memb && memb >
                carly) || (ystart(andy) < memb && memb < carly))
                    membmat(billy,carly,andy) = 0;
                end
            end
        end
    end
end
```

3. diffuse.m

```
%diffuse.m - SimRoots diffusion code - Nutrient moves down
concentration gradients across timesteps.

function [resland] = diffuse(resland,dmaster,xmax,ymax,d)
     %constant: 1/SQRT(2) used to speed up calculating distance
     between diagonally adjacent cells
     oosq2 = 0.70710678118654752440084436210485;
     tempresland = zeros(xmax,ymax);

     %dmaster sets how many iterations of diffusion should occur for
     each iteration of root dynamics
     for differ = 1:dmaster
          for andy = 1:xmax
               for billy = 1:ymax
                    holder = 0;
                    if andy - 1 > 0
                         if billy - 1 > 0
                              holder = holder +
                              d*oosq2*(resland(andy-1,billy-1,1)-
                              resland(andy,billy,1));
                         end
                         holder = holder + d*(resland(andy-
                         1,billy,1)-resland(andy,billy,1));
                         if billy < ymax
                              holder = holder +
                              d*oosq2*(resland(andy-1,billy+1,1)-
                              resland(andy,billy,1));
                         end
                    end
                    if billy - 1 > 0
                         holder = holder + d*(resland(andy,billy-
                         1,1)-resland(andy,billy,1));
                    end
                    if billy < ymax
                         holder = holder +
                         d*(resland(andy,billy+1,1)-
                         resland(andy,billy,1));
                    end
                    if andy < xmax
                         if billy - 1 > 0
                              holder = holder +
                              d*oosq2*(resland(andy+1,billy-1,1)-
                              resland(andy,billy,1));
```

```
                        end
                        holder = holder +
                        d*(resland(andy+1,billy,1)-
                        resland(andy,billy,1));
                        if billy < ymax
                              holder = holder +
                              d*oosq2*(resland(andy+1,billy+1,1)-
                              resland(andy,billy,1));
                        end
                  end
                  tempresland(andy,billy) = resland(andy,billy) +
holder;
            end
      end
      resland(:,:,1) = tempresland;
   end
end
```

4. resdyn.m

```
%resdyn.m - resource dynamics function - each plant takes up nutrient
based on its root presence, the root presence of any competitors, and
the nutrient concentration and uptake parameters of the landscape

function[resland, profit] = resdyn(resland, xmax, ymax, plantcount, u,
fcst, gamma, distmat)
     %uptake for each plant:
     roottotal = sum(resland(:,:,2:(plantcount + 1)),3);
     roottotal2 = roottotal;

     for andy = 1:(plantcount-1)
         roottotal2(:,:,andy+1) = roottotal;
     end
     totup = uptake(roottotal, resland(:,:,1)) .* u;
     totup2 = totup;
     for andy = 1:(plantcount-1)
         totup2(:,:,andy+1) = totup;
     end
     resland(:,:,1) = resland(:,:,1) - totup;
     prop = zeros(xmax,ymax,plantcount);

     prop(:,:,:) =
resland(:,:,(2:(plantcount+1)))./(roottotal2+.0000000000001);
     % the plus .0~01 just prevents divide by zero errors.
     nanfix = isnan(prop(:,:,:));
     prop(nanfix) = 0;
     up = prop.*totup2;

     income = sum(sum(up));
     costsa = resland(:,:,2:(plantcount+1)) * fcst;
     costsb = resland(:,:,2:(plantcount+1)) .* gamma .*
distmat(:,:,:);
     costs = costsa+costsb;
     profit = income-sum(sum(costs));
     profit = permute(profit, [2 3 1]);

     if sum(isnan(profit)) > 0
         up
     end
end
```

5. uptake.m

%uptake.m - the uptake function determines how much nutrient leaves
the cell based on current total root mass is present in the cell, with
diminishing returns

```
function [UpTot] = uptake(Root, Conc)
      for x = 1:(size(Root,1))
          for y = 1:(size(Root,2))
                c = Root(x,y) + Conc(x,y);
                cd = c * 2^.5;
                if Root >= Conc
                      dfc = (cd/2)-((c-Root(x,y))^2 + Conc(x,y)^2)^.5;
                else
                      dfc = (cd/2)-((c-Conc(x,y))^2 + Root(x,y)^2)^.5;
                end
                UpTot(x,y) = ((cd/2)^2-(dfc^2))^.5;
          end
      end
end
```

6. rootdyn.m

```
%rootdyn.m – root dynamics function: Each plant analyzes all of the
possible cells to grow root into, picks the best one, and grows root
into it.  They reiterate this process until either they have no
resource left with which to build root, or no profitable location for
root growth remains.

function [resland,pool] =
rootdyn(u,qr,pool,resland,fcst,gamma,xmax,ymax,plantcount,distmat,dmas
ter,d,psych,membmat,smell)
      oosq2 = 0.70710678118654752440084436210485;
      %constant: 1/SQRT(2) used to speed up calculating distance
      between diagonally adjacent cells
      flag = 0;
      [adj] = adjmat(resland(:,:,2:1+plantcount));
      adj2 = logical(resland(:,:,2:1+plantcount));

      %main loop: while at least one plant has enough resource to build
      more roots, and it hasn't decided not to (flag)
      while max(pool(:)) >= qr && flag < plantcount
            flag = 0;
            %temporary array of the benefits of growing into every cell
            tempGscape(:,:,:)=zeros(xmax,ymax,plantcount);
            %array to hold the proportion of roots in a cell,
            focal/total, if the focal organism decides to add to its
            root holding in that cell
            possprop(:,:,:) = zeros(xmax,ymax,plantcount);

            %total root mass in every cell
            roottotal=sum(resland(:,:,2:plantcount+1),3);
            roottotal2 = roottotal;
            for andy = 1:(plantcount-1)
                  %2 layers of total root mass
                  roottotal2(:,:,andy+1) = roottotal;
            end

            %run the uptake function for each plant
            totup=uptake(roottotal, resland(:,:,1)) .* u;
            totupTMP=uptake(roottotal, resland(:,:,1)) .* u;
            for andy = 1:(plantcount-1)
                  totup(:,:,andy+1) = totupTMP;
            end

            %calculate root proportions
```

```
        prop = zeros(xmax,ymax,plantcount);
        prop(:,:,:) = resland(:,:,(2:(plantcount+1)))./roottotal2;
        nanfix = isnan(prop(:,:,:));
        prop(nanfix)=0;
        for andy = 1:plantcount

possprop(:,:,andy)=(resland(:,:,1+andy)+qr)./(roottotal+qr);
        end

        %current intake from roots
        nowtot = prop.*totup;
        nowtotWhole = ones(xmax,ymax,plantcount);
        for andy = 1:plantcount
            nowtotWhole(:,:,andy)=sum(sum(nowtot(:,:,andy)));
        end

        %current expenses in root maintenence
        nowcost = fcst * resland(:,:,2:1+plantcount) +
        ((times(distmat, resland(:,:,2:1+plantcount))) * gamma);
        nowcostWhole = ones(xmax,ymax,plantcount);
        for andy = 1:plantcount
            nowcostWhole(:,:,andy) = sum(sum(nowcost(:,:,andy)));
        end

        %potential intake given root growth
        possup = resland(:,:,1) .* (roottotal+qr) * u;
        possupTMP = resland(:,:,1) .* (roottotal+qr) * u;

        for andy = 1:(plantcount-1)
            possup(:,:,andy+1) = possupTMP;
        end

        posstot = times(possup, possprop);

        %potential expense in root maintenance given root growth
        posscost = fcst * (resland(:,:,2:1+plantcount)+qr) + (gamma
        * (times(distmat, (resland(:,:,2:1+plantcount)+qr))));
        tempGscape = ((posstot - posscost) - (nowtot - nowcost) -
        (rand * .0000001)).*membmat;

        %remove possibility of growing into cells that aren't
        adjacent to or included in current root footprint
        tempGscape=times(tempGscape,adj);

        %find most profitable cell for growth
```

```
[rowmax, xindex] = max(tempGscape(:,:,:));
[colmax, yindex] = max(rowmax(:,:,:));

for andy = 1:plantcount
    xm(andy) = xindex(:,(yindex(andy)),andy);
end

%grow into it (assuming at least one profitable cell exists)
for andy = 1:plantcount
    if tempGscape(xm(andy),yindex(andy),andy)>0 &&
    pool(andy)>qr
        resland(xm(andy),yindex(andy),andy+1)=resland(xm(
        andy),yindex(andy),andy+1)+qr;
        pool(andy) = pool(andy)-qr;
    else
        flag = flag + 1;
    end
end
end

%The remaining code allows for the possibility of partial or
total root dieback when cost of maintenence exceeds nutrient
uptake within a cell

joy = ones(xmax,ymax,plantcount);
while sum(sum(joy(:,:,1:plantcount))) > 0
    flag = 0;
    tempGscape(:,:,:)=zeros(xmax,ymax,plantcount);
    possprop(:,:,:) = zeros(xmax,ymax,plantcount);
    roottotal=sum(resland(:,:,2:plantcount+1),3);
    roottotal2 = roottotal;
    for andy = 1:(plantcount-1)
        %2 layers of total root mass
        roottotal2(:,:,andy+1) = roottotal;
    end
    totup=uptake(roottotal, resland(:,:,1)) .* u;
    totupTMP=uptake(roottotal, resland(:,:,1)) .* u;
    for andy = 1:(plantcount-1)
        totup(:,:,andy+1) = totupTMP;
    end
    prop = zeros(xmax,ymax,plantcount);
    prop(:,:,:) = resland(:,:,(2:(plantcount+1)))./roottotal2;
    nanfix = isnan(prop(:,:,:));
    prop(nanfix)=0;
    for andy = 1:plantcount
```

```
    possprop(:,:,andy)=(resland(:,:,1+andy)-
    (qr))./(roottotal-(qr + .000000000001));
end

%allow possibility of NonSelf Recognition
if smell == 0
    prop = ones(xmax,ymax,plantcount)*1;
    possprop = ones(xmax,ymax,plantcount)*1;
end

nowtot = prop.*totup;
nowcost = fcst * resland(:,:,2:1+plantcount) +
((times(distmat, resland(:,:,2:1+plantcount))) * gamma);
possup = resland(:,:,1) .* (roottotal-(qr)) * u;
possupTMP = resland(:,:,1) .* (roottotal-(qr)) * u;
for andy = 1:(plantcount-1)
    possup(:,:,andy+1) = possupTMP;
end

posstot = times(possup, possprop);
posscost = fcst * (resland(:,:,2:1+plantcount)-(qr)) +
(gamma * (times(distmat, (resland(:,:,2:1+plantcount)-
(qr)))));
tempGscape = ((posstot - posscost) - (nowtot - nowcost) -
(rand * .0000001)).*membmat;
tempGscape=times(tempGscape,adj2);

[rowmax, xindex] = max(tempGscape(:,:,:));
[colmax, yindex] = max(rowmax(:,:,:));
for andy = 1:plantcount
    xm(andy) = xindex(:,(yindex(andy)),andy);
end
sig = sign(tempGscape);
manhattan = sig + 1;
manhattan = manhattan .* sig;
manhattan = logical(manhattan) * (qr);

brooklyn = resland(:,:,2:plantcount+1);
brooklyn = brooklyn - qr;
sig2 = sign(brooklyn);
brooklyn = sig2 + 1;
brooklyn = brooklyn .* sig2;
brooklyn = logical(brooklyn);

joy = and(manhattan, brooklyn);
```

```
            joy = joy * qr;
            for andy = 1:plantcount
                resland(:,:,1+andy) = resland(:,:,1+andy) -
joy(:,:,andy);
                resland(:,:,1) = resland(:,:,1) + joy(:,:,andy);
            end
        end
end
```

```
%adjmat.m - root matrix adjustment - generates a binary matrix the
size of the nutrient landscape with a layer for each plant: can this
plant choose to grow into this cell on this timestep?
%takes in a matrix with one root mass layer for each plant; returns a
binary matrix of the same size

function [matout] = adjmat(matin)
     tester = zeros(size(matin,1)+2,size(matin,2)+2,size(matin,3));

     tester2 = tester;

     %build a temporary matrix of the root values with an empty row of
     cells on all 4 sides of the root landscape
     for andy = 1:size(matin,1)
          for billy = 1:size(matin,2)
               for carly = 1:size(matin,3)
                    tester(andy+1,billy+1,carly) =
matin(andy,billy,carly);
               end
          end
     end

     %build a temporary matrix of the root landscape in which each
     cell contains the sum of the root mass in the focal cell and all
     8 surrounding cells
     for andy = 1:size(matin,1)
          for billy = 1:size(matin,2)
               for carly = 1:size(matin,3)
                    tester2(andy+1,billy+1,carly) =
                    sum(sum(tester(andy:andy+2,billy:billy+2,carly)))
                    ;
               end
          end
     end

     %get rid of the extra border rows from all 4 sides of the
     landscape
     for andy = 1:size(matin,1)
          for billy = 1:size(matin,2)
               for carly = 1:size(matin,3)
                    matout(andy, billy, carly) =
tester2(andy+1,billy+1,carly);
               end
          end
```

```
    end

    %simplify matrix to 1s & 0s: Does this plant either have root in
    this cell or in any adjacent cell?  If so, it will be permitted
    to choose to grow root here this timestep.
    matout = logical(matout);
end
```

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PUBLICATIONS

Poor Decisions About Security
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R Deric Leith Miller