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Intra-plant versus Inter-plant Root Competition in Beans: avoidance, resource matching or tragedy of the commons

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Abstract

Root competition inhibits root proliferation. All else equal, a plant should invest roots in a nutrient patch devoid of roots rather than one already occupied by roots. Less clear is how a plant should respond to intra-plant versus inter-plant root competition. We consider three responses for how a plant may select habitats based on intra-versus inter-plant root competition: inter-plant avoidance, resource matching, or intra-plant avoidance. The first assumes that plants prefer to have their own space and preferentially proliferate roots away from neighboring plants. The second response, based on the ideal free distribution, assumes that plants invest so as to equalize average returns from roots, regardless of the identity of the neighboring roots. The third, based on game theory, assumes that the plant proliferates roots so as to maximize whole-plant fitness, in which case it is better to proliferate plants among a neighbor's roots than to continue proliferating amongst one's own roots. To test among these models we grew beans (*Phaseolus varigaris*, var. Kenya) in a greenhouse under two planting scenarios. Both scenario were tested under 0.5 and 0.1 strength of nutrient solution. Under scenario A (fence-sitters), two split-root plants each shared two patches by virtue of having roots in each. Under scenario B (owners) two plants each had their own patch. The results supported the game theory model of intra-plant avoidance (whole plant habitat selection). Fence-sitters produced 150% more root mass per individual than owners. Owners produced 90% more yield (dry mass of pods) than fence-sitters. Furthermore, owners had significantly higher shoot-root ratios than fence-sitters. These effects did not vary with high or low nutrient levels. The over-proliferation of roots under inter-plant competition (fence-sitters) was manifest by the tenth day after planting. In short, the fence-sitters engaged in a tragedy of the commons in which they competed with each other through root proliferation. At the ESS, the fitness maximizing strategy of the individual is to sacrifice collective yield in a quest to 'steal' nutrients from its neighbor. The research has three implications. First, plants may be able to assess and respond to local opportunities in a manner that maximizes the good of the whole plant. Second, nutrient foraging as a game may provide a fresh perceptive for viewing root competition either intra-specifically or inter-specifically. Third, it may be possible to increase the yield of certain crop species by breeding more 'docile' cultivars that do not overproduce roots in response to inter-plant competition.

Introduction

Habitat selection, the study of how organisms assess and respond to habitat heterogeneity (Brown 1998), considers how organisms should allocate time or effort in response to variability in hazards, opportunities and competitors (Rosenzweig 1985; Brown 1998). Theories of habitat selection have generally been developed for mobile and behaviorally sophisticated animals (Brown & Rosenzweig 1986; Rosenzweig 1991; Morris 1994). Yet, plants exhibit habitat selection (Bazzaz 1991). A recent surge of interest in habitat selection in plants has revealed that plants have the capacity to adjust their structure and physiology to small scale variation in resource levels. For example plants select habitats through flexible root growth in response to spatial and temporal variability in soil nutrients (Hackett 1972; Drew & Saker 1975; Campbell et al. 1991). The above ground shoots also respond to favorable light conditions by forming leaves and branches more rapidly. Root allocation can be quite sophisticated as shown by plants directing roots away from competitors (Gersani et al. 1998). The phenotypic plasticity of plants becomes analogous to the foraging strategies of animals. Plants can be thought of as foraging for light, rich micro-sites in the environment and escape from competition.

The quality of a patch of soil should include nutrient and water availability, favorability of soil texture and porosity, above ground potential for light and space, and the presence of other active roots. All else equal, a plant should prefer to invest roots in a nutrient patch devoid of active roots than an already occupied patch. Root competition should inhibit root proliferation. What is less clear is how a plant should respond to the intra-plant versus inter-plant root competition. Should a plant prefer to proliferate roots in a patch that it already occupies, or should it prefer a patch occupied by the roots of another individual? There are three responses for how a plant may select habitats based on intra- versus inter-plant root competition: inter-plant avoidance, resource matching, or intra-plant avoidance.

Inter-plant avoidance may result from resource depletion or from plants exhibiting a form of territoriality. In a consumer-resource model of root competition, Novoplansky and Cohen (1997) predicted that plants may create a zone of depletion in their neighborhood that precludes other plants from profitably foraging for nutrients. By reducing resources to below competitors' thresholds of profitability, inter-plant competition may encourage almost complete segregation of roots among individuals. Or, plants may directly recognize the presence of competitors. Ballare et al. (1987) suggested that some species avoid areas where they would experience interference even before they are in physical contact with neighbors. There is some support for self- non-self recognition and subsequent root proliferation away from inter-plant competitors (Mahall & Callaway 1991, 1992). Based on these sorts of recognition mechanisms, D'Antonio & Mahall (1991) suggested that plants may become territorial by proliferating roots with the intent of directly discouraging intrusions from other individuals. Within the root system, the development of different axes of growth is coordinated. However, some researchers have suggested inhibitory effects that regulate growth in some parts of plants and promote growth in other parts (Wightman & Thimann 1980).

In this study, we consider three models of habitat selection for how a split-root bean plant should allocate root growth between two equal habitats. The first views plant as 'competing populations of redundant organs' in which successful combinations of roots and shoots grow more rapidly at the expense of less prosperous units (Sachs et al. 1993). Under this passive process, the plants would simply reinvest more root growth back to the roots that provided more nutrients. The second views root allocation in plants as analogous to density-dependent habitat selection and ideal free distribution (Fretwell & Lucas 1970). The plant distributes root growth among nutrient patches so as to equalize the average rate of nutrient uptake per unit investment in roots (Gersani et al. 1998).

We propose a third model, centrally-planned habitat selection, in which we consider root allocation and habitat selection as a behavioral game (Brown 1998, Gersani et al. *in press*). As a game, habitat selection by individual plants does not necessarily result in combinations of strategies among individuals that are pareto optimal – solutions in which it is not possible to further benefit everyone (Brown 1998). Instead, the plant allocates root growth so as to maximize the common good of the whole plant in response to its own roots and the roots of others. Of these three means of root allocation, the first comes closest to the conventional wisdom on plants and the third provides the most behaviorally sophisticated game of habitat selection. We had three goals in these experiments: to apply the theory to Kenyan beans; to investigate the role of nutrient concentration; and to investigate the timing (age) when inter plant root competition begins to influence root production and the root/shoot ratio (allocation of resources).

Predictions

We consider a plant that must 'decide' how to allocate roots between two soil habitats. Factors influencing this decision may include the richness of each habitat (devote more roots to rich than poor soil patches; Gersani & Sachs 1992), and the presence of competitors (devote more roots to uncrowded than crowded soil patches; Gersani et al. 1998). We considered the first two scenarios in Figure 1 (A and B). Each scenario has two plants and two habitats. Under scenario A (fence-sitters), two plants each share two habitats by virtue of having roots in each. Under scenario B (owners), two plants each have their own habitat. While each scenario has the same number of plants, the same total space, and the same total amount of nutrients, scenario A involves both inter-plant and intra-plant root competition, scenario B only involves intra-plant root competition. To generate predictions, we assume that the total rate of nutrient uptake increases at a diminishing rate with the total root mass in a habitat. We assume that fitness or fruit production increases monotonically with net nutrient uptake where some nutrients are lost to the maintenance of roots and shoots. Finally, we assume that plants sharing the same habitat acquire resources in proportion to their root mass. In any of these models, root architecture or physiology could be substituted for strict rootmass.

The models deal with any phenotypically plastic trait by which plants can, for a price, increase their rate of nutrient uptake. Because the following experiments only measured total root mass we will restrict the predictions to this response, although it would be of considerable interest to know whether the plants also responded to the experiments in terms of ratio of fine roots to main roots, or altered uptake kinetics.

Avoidance of inter-plant competition

If plants actively avoid sharing space with competitors, or if they produce allelopathic chemicals to retard a competitor's root production then we can make the following predictions regarding root production and yield for the two scenarios. Avoidance may be so complete that each fence-sitter relinquishes a habitat to the other (as predicted in Novoplansky & Cohen 1997). In this case, the nutrient foraging behaviors of the individual plants will reduce the fence-sitters of scenario A to the owners of scenario B. This perspective predicts that fence-sitters will segregate roots so extremely that each will become an owner in one if its habitats. Hence, root production per individual plant should be the same for the fence-sitters as for the owners. Yield per individual should be the same for fence-sitters and owners (Table 1).

Avoidance may not be so extreme. Both plants may proliferate roots in both habitats, but curtail root production as a consequence of segregation within a habitat, allelopathy, or other strongly inhibitory effects of inter-plant root competition. In terms of reducing root proliferation, the plants will overcompensate (Schenk et al. 1999). This perspective predicts that segregation of roots may occur within habitats, but not among habitats. In terms of root production per individual, fence-sitters should produce less than owners. Stated another way, there should actually be fewer total roots within a habitat when plants are grown as fence-sitters than as owners. In terms of yield per individual plant, the overcompensation of plants to inter-plant competition or to allelopathy should cause a sacrifice in the yield of fence-sitters relative to owners. Alternatively, if space itself is a non-depletable resource (McConnaughay & Bazzaz 1991, 1992), then the fence-sitters may produce higher yields than owners because each fence-sitter has twice as much space as each owner (Table 1).

Resource matching and an Ideal Free Distribution

Gersani et al. (1998) discussed how a plant exploitatively competing for nutrients may distribute roots in accord with an ideal free distribution (Fretwell & Lucas 1970). Total root proliferation of individuals within a habitat might match the availability of resources. In this way, average nutrient uptake per unit rooting effort is equalized across space. If roots of different individuals have the same opportunity for nutrient uptake, then a plant's decision of where to proliferate should be independent of whether root competition is intra-plant or inter-plant. The plant's decision should be based solely on the total amount of roots it has already produced (insofar as this influences the marginal cost of producing additional roots) and the nutrient uptake opportunities in each habitat (determined by the ratio of nutrient availability and the total of all individuals' roots exploiting the habitat). In terms of root segregation, roots of the same or of different individuals should have the same inhibitory effect on an individual's root proliferation. In terms of root production or yield per individual there should be no differences between fence-sitters or owners. If, however, space is a non-depletable 'resource' independent of water and nutrients, then fence-sitters should produce more roots and more yield per individual than owners.

Intra-plant avoidance: Whole plant habitat selection

If plants are able to make a whole-plant response to the nutrient foraging opportunities presented by the two habitats, then the fence-sitter scenario can be modeled as a 2-person game of nutrient foraging and the owner scenario is a one-player game. Both scenario consider a symmetric competition. The format

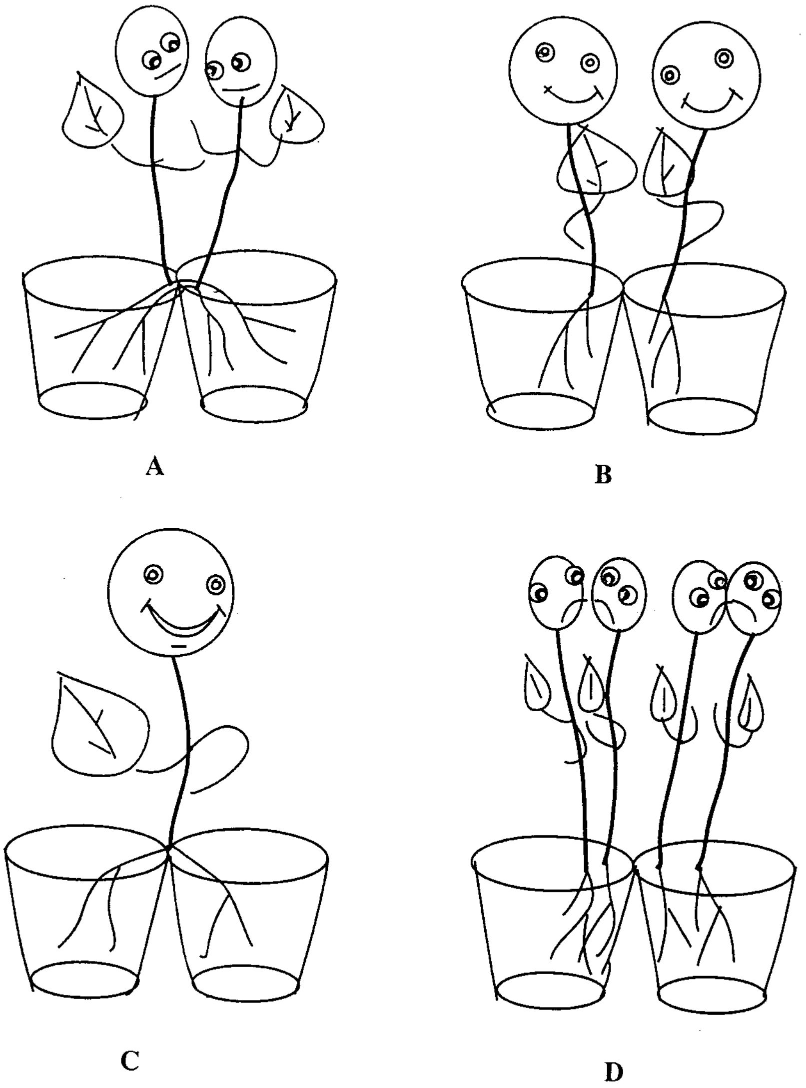

Figure 1. The two scenarios of habitat selection. Scenario A (fence-sitters) represents a two player game in which two plants each have roots in both habitats/pots. Scenario B (owners) represents a one player game in which each plant has all of its roots in its habitat/pot. Scenario C (single fence-sitter) represent one plant straddling two pots, and scenario D (two owners) represent two plants restricted to a single pot.

Table 1. Summary of the predictions of each model in terms of root segregation, root mass and yield. The models and variants are: inter-plant avoidance with complete segregation. inter-plant avoidance with partial segregation. resource matching when soil space is a separate non-depletable resource, and intra-plant avoidance from habitat selection by the whole plant.

Model	Roots production	Yield production
Inter-plant avoidance with complete segregation	Fence-sitter = Owner	Fence-sitter = Owner
Inter-plant avoidance with partial segregation depletable resource	Fence-sitter < Owner	Fence-sitter < Owner
Resource matching	Fence-sitter = Owner	Fence-sitter = Owner
Resource matching when soil space is non-depletable resource	Fence-sitter > Owner	Fence-sitter > Owner
Intra-plant avoidance (whole plant habitat selection)	Fence-sitter > Owner	Fence-sitter < Owner

model can be found in Gersani et al. (*in press*). Here, we will describe the model's logic and results. Under both scenarios, a plant behaving optimally should produce roots until the marginal benefit of additional roots no longer exceeds the marginal cost of roots. First consider the owner. The marginal benefit of additional roots has a positive and negative component. The additional roots will contribute some nutrients. However, some of these contributed nutrients may not be new uptake but rather represent nutrients that would have been harvested by the individual's preexisting roots. To the whole plant, the net benefit of new roots only includes new nutrients rather than those 'stolen' from the plant's other roots. Second, consider the fence-sitters. The marginal benefit of additional roots includes new nutrients and the nutrients stolen from the other plant's roots. Hence, for the same total root density in a habitat, a fence-sitter will perceive a higher marginal value to root proliferation than an owner. The plant perceives stealing nutrients from a neighbor as a positive whereas stealing from oneself is perceived as a negative.

In other words, from the whole plant's point of view, intra-plant root competition should discourage root proliferation more than inter-plant root competition. All else equal, a plant should proliferate roots into a virgin habitat first. But, given the choice between a habitat already occupied by its own roots and one occupied by another's, a plant should prefer to proliferate roots under inter-plant than under intra-plant competition (this preference is also found in models where seed dispersal is in response to sib-sib competition, e.g. Venable & Brown 1993). As a one player game, the plant produces roots so as to maximize the net nutrient gain from its habitat. This will also maximize yield. As a two player game, the plant overproliferates roots beyond that which would maximize net nutrient harvest from the habitat. The fence-sitters engage in a tragedy of the commons (Hardin 1968). At the ESS, each plant over-produces roots in response to other. Why? Because a fence-sitter that did not would be in even worse shape in terms of yield, if it let the other plant take advantage of its restraint. In response to the presence of a competitor's roots a plant's yield-maximizing strategy is to produce more roots than it would if the other competitor's roots were its own. Of course, the other fence-sitter should respond in kind. The advantage of stealing nutrients from one's neighbor drives the plants to overproliferate roots and into a tragedy of the commons where paradoxically they both produce less yield than they could have had they both shown restraint.

Whole plant habitat selection where the individual avoids intra-plant competition, predicts that the fence-sitters will have highly inter-twined root masses in both habitats, as each individual perceives more benefit from engaging in inter-plant than intra-plant root competition. In terms of root mass per individual, fence-sitters should produce more than owners. On a per habitat basis, there should be more total roots in a habitat under the fence-sitter than under the owner scenario. In terms of yield per individual, owners should produce more seed mass than fence-sitters (Table 1).

In terms of root segregation, root mass, and yield each model and its variants makes a unique set of predictions. The models and variants are: Inter-plant avoidance with complete segregation, inter-plant avoidance with partial segregation, resource matching, resource matching when soil-space is a non-depletable resource, and intra-plant avoidance from habitat selection by the whole plant.

Methods

The bean, *Phaseolus varigaris* (var. Kenya), has been cultivated extensively in dry areas of Kenya. It is generally mix-cropped with maize. We chose this bean for three reasons. First, it is a legume with large seeds for which the split-root techniques of the following experiments are well suited. Second, it provides a close comparison for our previous work with soybeans (Gersani et al. *in press*). Third, it is agriculturally important for Kenya. The use of a cultivar in these experiments has advantages. If cultivars that have been bred specifically for high yield exhibit the tragedy of the commons from engaging in a two-player or n-player game of root competition, then it is very likely that wildtype plants will exhibit the same. And, if cultivars do exhibit the tragedy of the commons, then the results of the experiment reveal opportunities for breeding higher yielding, more docile (with respect to root competition) crops.

Phaseolus varigaris (var. Kenya) were grown in a greenhouse at the University of Illinois at Chicago for two experiments. The first experiment lasted from 24 January to 24 March 1997, and the second from 15 October to 16 December 1997. For each experiment the seeds were first soaked for 24 hours in aerated water and then sown on vermiculite with their radicle facing down. After 24–48 h, when the roots were about 10 mm long, the distal 1–2 mm of the single root of each seedling was removed and the seeds replanted. This caused the single root to proliferate lateral roots. This variety of beans produces bunches of roots from the cut surface. In this way, we created a split-root system that contained two equal root masses. We transplanted seedlings into plastic pots (18 cm diameter × 20.6 cm height) filled with vermiculite. The pots were placed on four benches in the greenhouse.

Each experiment had two planting scenarios: (i) each of the 2 split-root plants were planted in separate adjacent pots (fence-sitters, Figure 1a), (ii) each of the 2 split-roots were planted in one pot (owner, Figure 1b). The pots were saturated every three days with Hoagland nutrient solution (Hoagland & Arnon 1950). The total amount of nutrient solution supplied to each plant was 1.6 l per watering period. This was made possible by running an irrigation system with nutrient solution for 12 min. The excess solution drained through holes at the base of the pot. In order to reduce chances of salt accumulation, after every two waterings with nutrient solution, plants were watered with distilled water for 16 min to flush nutrient salts from the pots.

In addition to the planting treatments, we applied 2 levels of nutrient concentration. Each pot of a pair received either 0.5 or 0.1 strength Hoagland's nutrient solution. We used drip irrigation to ensure that all pots received the same supply of solution. To factor out effects of location on benches in greenhouse, 4 pairs of pots constituted a block. Within a block, all 4 combinations of planting treatment and nutrient concentration were present among the pairs of pot. The pairs of pots within blocks were randomized, and therefore the above ground competition was randomized. That meant each plant, either an owner or a fence-sitter, faced similar above ground competition as the either plant had neighbors at similar distances. The pots were notched so that plants were not sitting directly on the pot edge. Gersani et al. 1998 discusses how a split-root plant standing on the pot is not compromised by the treatment.

Experiment 1

In the first experiment, the objective was to test among the models of how plants might respond to intra- versus inter-plant root competition. We sowed 25 blocks of plants with all combinations of nutrient concentration and planting treatment (fence-sitters vs. owners) present within each block.

We planted four additional blocks to investigate some of the assumptions of the model. In four of the blocks we sowed just a single fence-sitter straddling the pair of pots (Figure 1c). This treatment tests whether pairs of plants in the fence-sitter treatment are negatively affected by competition, and it tests whether the owners with just one pot experience nutrient limitation. If the plants in our experiments are experiencing competition as fence-sitters and nutrient limitation as owners, then the single fence-sitters should produce (per individual) more roots and more yield than either the fence-sitters or the owners. Two plants in each block received 0.1 strength solution in both of their pots and two plants received 0.5 strength. The size and success of the single fence-sitters relative to the fence-sitters and owners should occur at both nutrient levels.

Another four blocks investigated the effects of skewed nutrient availability. Three of the pairs of pots contained a single fence-sitter straddling two pots. One pot received 0.1 strength solution (low quality habitat) and the other pot received 0.5 strength solution (high quality habitat). If habitat quality matters and the plants respond accordingly, then a plant should, invest more roots into the high quality pot. Furthermore, the plant's total root mass and yield should fall somewhere in between that of single fence-sitters exposed to 0.5 strength only and 0.1 strength only. The fourth pair of pots in these blocks was devoted to further seeing the negative effects of nutrient limitation and inter-plant competition. One pot received 0.1 strength and the other 0.5 strength nutrient solution. In each pot we planted two seedlings (Figure 1d). Relative to owners, these plants are disadvantaged by having inter-plant as well as intra-plant competition. Relative to fence-sitters, these plants are disadvantaged by having half as much space per individual. When two plants share a single pot, they should produce (per individual) less yield and less root mass than either fence-sitters or owners.

We harvested the plants after 60 days on 24 March 1997. After oven drying, we measured the dry-mass of each plant's pods, seeds, roots, and shoots (stem and leaves). We also counted the numbers of pods and seeds.

Experiment 2

In the second experiment, our objective was to investigate at what stage of growth the plants begin to exhibit different patterns of growth in response to the fence-sitter and owner planting scenarios. For this experiment, we planted 36 blocks with all combinations of high- and low-concentration nutrient solution and planting treatments of fence-sitters versus owners. (This experiment did not include any additional blocks with single fence-sitters or with pairs of plants sharing a single pot). At regular intervals of 5, 10, 20, 40, 50 and 60 days after planting we harvested six blocks of plants per time interval. At each interval we selected five blocks at random from the pool of remaining blocks. At 60 days plants and seeds were mature. From each plant harvested we oven dried its parts and measured the drymass of pods, seeds, leaves, stem and roots. Pods and seeds were present on only those plants harvested at the 40 (small and immature pods and seeds), 50 (some ripening of pods and seeds) and 60 (fully ripe) day intervals. We also counted the numbers of pods and seeds.

Results

Experiment 1: Fence-sitters versus Owners

We used a three-way MANOVA to test for the effects of planting treatment (fence-sitter versus owner), nutrient concentration, and blocks on rootmass, podmass, shootmass, pod number, and mass per pod (podmass/pod number) (Table 2). To normalize the data and better fit the assumptions of the model, we logarithmically transformed data on rootmass, podmass, shootmass and mass per pod; and we square root transformed data on pod number.

The results strongly support the game theory model of whole plant habitat selection (Gersani et al. *in press*). The data show intra-plant avoidance and a tragedy of the commons under inter-plant root competition (Figure 2). In the fence-sitter treatment, each individual proliferated roots in each pot and the roots of each individual were tightly intertwined. There was no visual evidence for inter-plant root segregation either among or within pots. Fence-sitters produced significantly more (150% more) roots per individual than owners. This effect occurred as strongly at both nutrient concentrations. Owners produced significantly more field per individual than fence-sitters. Owners produced 90% more podmass, 53% more pods, and 18% more mass per pod than fence-sitters. Owners and fence-sitters did not differ in shootmass per individual. All of the above effects were independent of nutrients. There were no significant interactions of nutrient concentration with the planting treatments of owners versus fence-sitters.

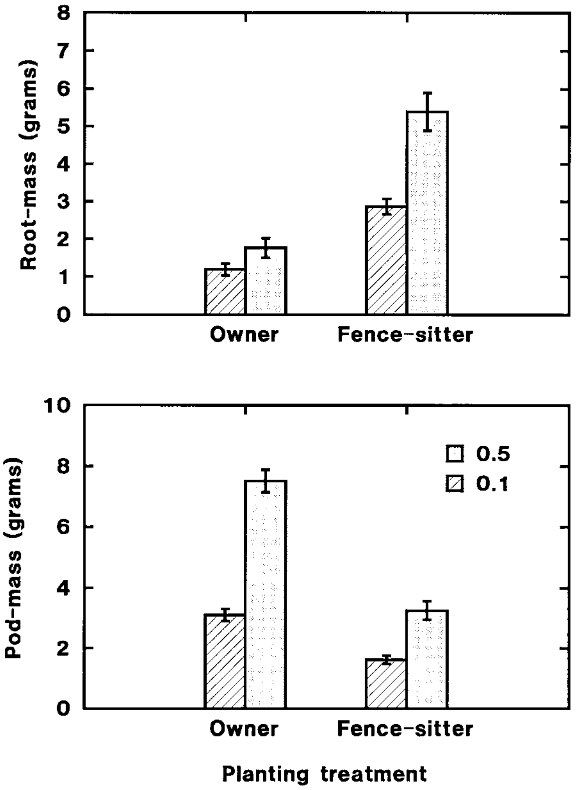

Figure 2. Intra-plant avoidance and a tragedy of the commons under inter-plant root competition. Owners produced less roots per individual plant than fence-sitters. Owners produced more pods than fence-sitters. These results were independent of nutrient concentration.

The five-fold increase in nutrient concentration produced an 85% increase in rootmass, a 110% increase in shootmass, a 125% increase in pod mass, and a 130% increase in pod numbers. Nutrient concentration had no effect on the average size of a pod (Figures 2 & 3).

To compare owners and fence-sitters with respect to shoot-root ratios, we used an ANOVA with a logarithmic transformation of shoot-root ratio as the dependent variable and planting treatment, nutrient concentration and block as independent, categorical variables. As would be expected for a plant foraging for essential nutrients (light and minerals) in different places (above- and below-ground) (Vincent et al. 1996), shoot-root ratios increased with nutrient concentration ($F_{1,109} = 8.54$, $P < 0.005$). In accord with the whole plant response to interspecific competition, fence-sitters had significantly lower shoot-root

Table 2. For experiment 1, a three way MANOVA table showing the effect of plant treatment (fence-sitter versus owner), nutrient concentration, and block on rootmass, podmass, shootmass, pod number, and mass per pod.

Variable	d.f.	Rootmass	Podmass	Pod number	Shootmass	Mass/pod
Concentration (C)	1	41.8***	143.43***	101.76***	121.54***	0.003
Treatment (T)	1	160.02***	126.31***	28.08***	0.32	5.92*
Block	21	0.97	3.37***	1.20	3.61***	1.69*
C*T	1	2.41	1.94	7.68**	0.22	0.31
C*Block21	1.23	1.48	0.99	1.09	1.29	
T*Block	21	3.52***	2.11**	0.98	1.36	1.32
Error	109	0.274*	0.193*	7.85*	0.228*	0.169*

# indicates error mean sum of squares.
$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

ratios than owners ($F_{1,109} = 97.8$, $P < 0.001$). As evidence for the striking behavioral response of the plants to inter-plant competition, a five-fold increase in nutrient concentration produced a much smaller effect on shoot-root ratios and plant architecture than a shift from intra- to inter-plant competition (Figure 3). Despite the significant interaction effect between block and planting treatment ($F_{21,109} = 1.74$, $P < 0.05$), owners exhibited higher shoot-root ratios than fence-sitters in all but one of the 22 blocks.

Experiment 1: Evidence for competition

To test the assumption of resource competition and inter- and intra-plant competition we grew some additional blocks of plants as either single fence-sitters (one plant straddling two pots) or as two individuals restricted to a single pot. The former treatment allows the plant to have more space and to be an owner. The latter treatment forces the plant into less space and into inter-plant competition. On a per individual basis, we used a MANOVA to test for the effects of planting treatment (single fence-sitter, owner, fence-sitter, and two plants in a single pot) and nutrient concentration on logarithmically transformed data on rootmass, shootmass, and podmass. In terms of rootmass: fence-sitter (3.93 g = single fence-sitter (3.64 g) > owner (1.44 g) > two plants in a pot (1.28 g). In terms of shootmass: single fence-sitter (4.93 g) > fence-sitter (2.08 g) = owner (1.99 g) > two plants in a pot (0.76 g). In terms of podmass: single fence-sitter (7.03 g) > owner (4.82 g) > fence-sitter (2.29 g) = two plants in a pot (1.80 g) (Tukey post-hoc comparisons, significant at the $P = 0.05$ level, at least). While rootmass, shootmass and podmass all increased with nutrient concentration, the effect of planting treatment was independent of nutrient concentration.

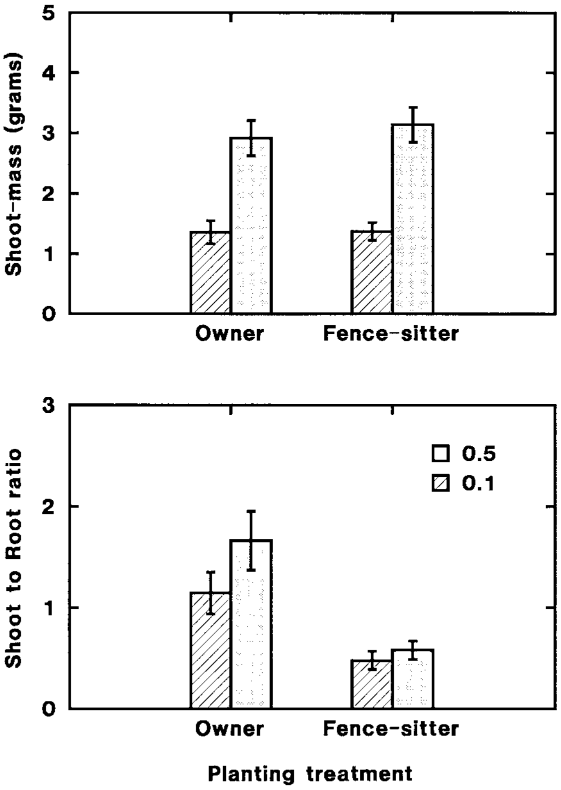

Figure 3. The effect of planting treatment (owner versus fence-sitter) on shootmass. Owners and fence-sitters did not differ in shootmass per individual. However, in accordance with whole plant responses to inter-specific competition, fence-sitters had lower shoot-root ratios than owners.

Pairs of plants were similar in size. There was no evidence that one plant of a pair dominated the other, thus creating a large asymmetry in size. However, the planting treatment may influence the symmetry in size among pairs as owners were competing only for light from separate pots and fence-sitters were competing

Table 3. For Experiment 2, a four-way MANOVA showing the effect of age, nutrient concentration, planting treatment (fence-sitter versus owner), and block (nested within age) on rootmass and shootmass.

Variable	d.f.	Shootmass F	Rootmass F
Treatment	1	1.22	4.10*
Concentration	1	37.07***	6.41*
Age	5	250.03***	99.06***
Concentration*treatment	1	1.31	0.00
Age*treatment	5	1.14	1.37
Concentration*age	5	3.11**	1.16
Block (age)	29	2.14**	2.07**
Error	232	0.262#	0.413#

#indicates error mean sum of square.
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

for light and nutrients over the combined space of two pots. We used a three war MANOVA to test for the effects of planting treatment, nutrient concentration and block on the variance in root mass, shoot mass, and pad mass between pairs of plants. To factor out the effect of overall magnitude, we calculated the variance on log-transformed data. Most effects were not significant. In terms of root mass, individuals from a pair of owners had significantly higher variance than fence-sitters ($F_{1,21} = 17.29$, $P < 0.001$). In terms of pod mass, individuals from a pair of fence-sitters had significantly higher variance than owners ($F_{1,21} = 4.54$, $P < 0.05$). Nutrient concentration influenced only the variability in roots, with higher variance at high nutrient concentration than at low concentration ($F_{1,21} = 4.85$, $P < 0.05$). There were no significant interaction effects among planting treatment, concentration and block.

Experiment 2: Effect of age on intra-versus inter-plant root competition

We used a four-way MANOVA to test for the effects of age, nutrient concentration, planting treatment (fence-sitter versus owner), and block (nested within age) on rootmass and shootmass (Table 3). We used a three-way ANOVA (like experiment 1) to test for the effects of planting treatment, nutrient concentration and block on the yield of the plants harvested during the last time interval (60 days).

Encouragingly, the results again supported the model of whole plant habitat selection with intra-plant avoidance and a tragedy of the commons under inter-plant competition. Fence-sitters produced significantly more roots per individual than owners (Figure 4). Remarkably this effect was already manifest by the 10th growing day and persisted through all remaining time intervals (no significant interaction between planting treatment and age). By the 10th day the roots of the different individuals had occupied only a fraction of the available space in the pot, yet the fence-sitters were already over-proliferating roots relative to the owners. There was no difference between owners and fence-sitters in shoot-mass. Owners at 60 days of age produced significantly greater pod mass than fence-sitters (Figure 5). The five-fold increase in nutrient concentration produced a 21% increase in rootmass,

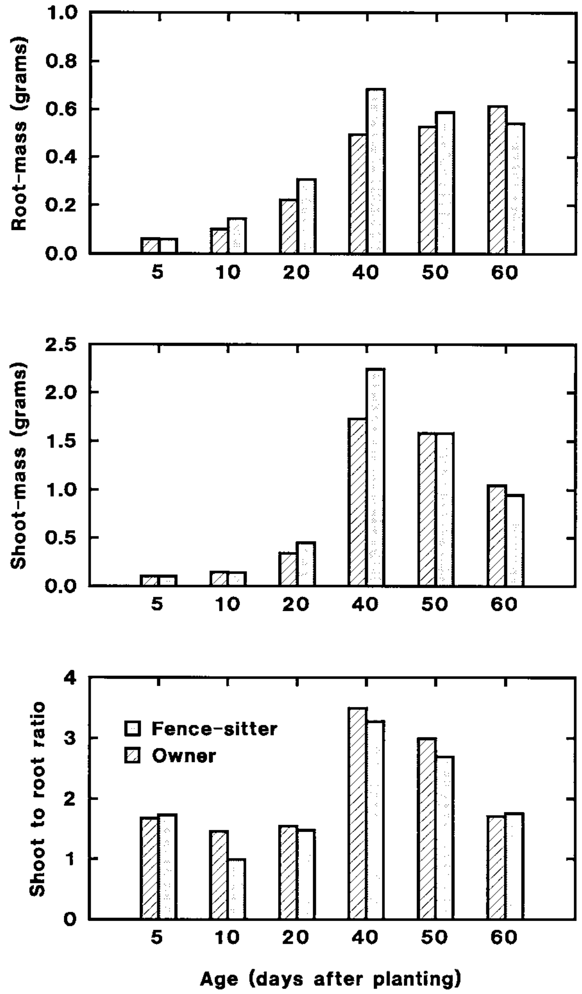

Figure 4. The effect of age on intra- versus inter-plant root competition. Fence-sitters produced significantly more roots per individual than owners. This effect is already manifest by the 10th growing day and persists through all remaining time. However, there was no difference between owners and fence-sitters in shootmass. Owners had higher shoot-root ratios than fence-sitters (although this effect was not significant).

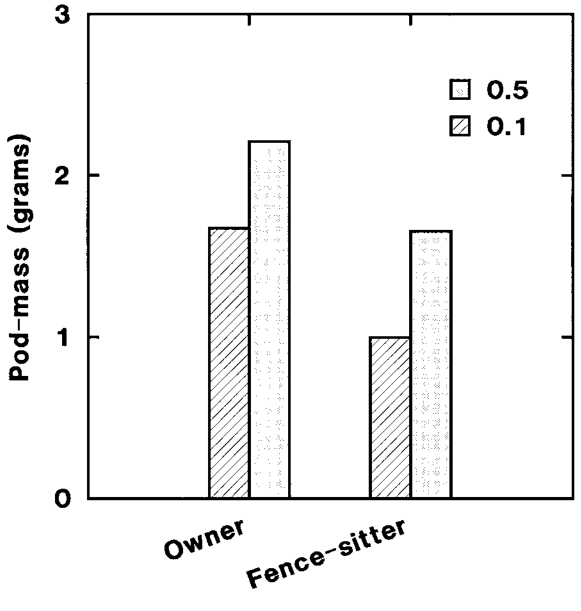

Figure 5. The effect of planting treatment (owner versus fence-sitter) on pod production. Owners at 60 days of age produced more yield (podmass) than fence-sitters which is in accordance with whole plant responses.

Table 4. ANOVA table showing the effect of planting treatment, nutrient concentration and age on the shoot-root ratio.

Variable	d.f.	MSS	F
Root	1	72.11	10.4.96***
Treatment	1	0.06	0.09
Concentration	1	14.70	21.40***
Age	5	13.61	19.82***
Concentration* Age	5	5.35	7.79***
Error	266	0.69	

***indicates $P < 0.001$

a 32% increase in podmass, and a 45% increase in shootmass. There were no significant interaction effects, none of the three potential interactions among nutrient concentration, age, and planting treatment influenced results.

To test for the effects of planting treatment, nutrient concentration and age on shoot-root ratios, we used an ANOVA with blocks nested within age (Table 4). As before, owners had higher shoot-root ratios than fence-sitters (although this effect was not significant). Also, shoot-root ratios increased significantly with nutrient concentration. The effect of age was more complicated. Shoot-root ratios declined markedly from 5 to 10 days, at which point they increased dramatically until day 40. At day 40, they again declined significantly until day 60. There were no significant interaction effects among the three independent variables.

It is worth noting that the direction of the response of experiment 2, even when statistically nonsignificant, were in the direction expected and as in experiment 1 for significant treatment effects. Lack of significant results may be due to small sample sizes as in experiment 1.

Discussion

We used split-root seedlings of beans planted as either owners (one plant per pot) or fence-sitters (two plants sharing two pots) to test for different responses of plants to either intra-plant (owner) or inter-plant (fence-sitters) root competition. This allowed us to test among several models and perspectives on root competition within plants (Table 1). The owners were strikingly different from the fence-sitters in their growth and resource allocation to different plant tissues. Relative to fence-sitters, owners produced much less root mass, more yield, and higher shoot-root ratios. In this respect, the plants under inter-plant competition engaged in a tragedy of the commons (Gersani et al. *in press*). Each fence-sitter in response to competition over-produced roots beyond that which would maximize yield. The differences between owners and fence-sitters in rootmass and shoot-root ratios were already pronounced by the 10th day of planting. Neither age of plant nor nutrient concentration influenced the different responses of plants to intra- versus inter-plant root competition. All of these results support the predictions that come from considering root competition as a game among individual plants. At the ESS, plants should respond to inter-plant root competition by overproducing roots and sacrificing yield relative to what they should do in the absence of inter-plant competition. Our results support the view that these plants coordinate their allocation of resources in a manner that promotes the whole plant.

These results are in accord with a small and growing body of literature on the subject. Gersani et al. (*in press*) used split-root soybeans to examine the plants' responses to intra-plant competition (owners) and inter-plant competition (fence-sitters). Just as in our present experiment, the soybeans produced more roots and less yield under inter-plant competition than under intra-plant competition. Interestingly, the beans responded even more dramatically than the soybeans. The more aggressive response of the Kenyan beans to inter-plant competition may lie in cultivation techniques. Soybeans have been selected for and are grown as monocultures of closely spaced plants (10 cm between plants in a typical soybean field). Kenyan beans are typically mix-cropped with maize and grown at distances in excess of 20 cm from each other. Relative to soybeans under cultivation, the typical Kenyan plant may share less of its space with neighbors. Like the soybeans, the Kenyan beans change their allocation pattern in response to inter-plant competition. Fence-sitters had lower shoot-root ratios than owners.

Our experiment allowed us to investigate the timing of effects. The plants' response to inter-plant competition is manifest by the 10th growing day in the pots. Accelerating root production in response to a neighbor occurs long before the available space in the pot has been occupied, and even before there is conspicuous overlap in root systems. Furthermore, investment in roots remains steady throughout the full 60 days. However, there is a significant decline in shoot-root ratios after ca. 50 days. It appears that the plants make a relatively complete shift to fruit production at about 40 days, at which point root mass is maintained and shootmass becomes partially reallocated to fruit production.

Support for the whole-plant model of habitat selection has interesting conceptual and empirical ramifications. Conceptually, we considered three broad views on how plants might respond to root competition. One of these suggests that plants avoid inter-plant root competition relative to intra-plant competition either as a means of maximizing exclusive space or in response to the direct negative consequences of allelopathy. Without a clear model of fitness and an analysis of what rooting strategy would maximize fitness in response to a nutrient-foraging game of root competition, it is not obvious when this perspective should prevail. A second perspective has the plant allocating roots to different nutrient patches in accord with the expectations of resource matching and the ideal free distribution (Gersani et al. 1998). Roots are allocated among patches until the average uptake rate per unit rooting effort is balanced among patches. In this case, intra- and inter-plant root competition have the same effect on a plant's average uptake rate per unit root. In this case, root production should be in response to the total existing amount of roots and their effect on nutrient availability, and not on the specific identity of the roots with respect to individual. This is a sensible strategy on the part of a plant that cannot distinguish its own roots from the roots of its neighbors (no self- non-self root recognition mechanism), or for a plant that cannot exercise an integrated, whole-plant response to local opportunities for nutrient foraging. Neither of the above two perspectives were supported by the data.

If the plant is capable of a whole-plant, integrated response to local opportunities, then local root allocation should promote the fitness of the whole plant. Rather than equalizing average returns among different resource patches (like resource matching), the plant should equalize the marginal returns among patches (incremental benefit from producing an incremental amount of new roots). In response to intra-plant root competition. the marginal benefit of increased root production includes the uptake of the new roots minus uptake that has been 'stolen' from other roots of the same plant. There is no point to the plant in producing roots that up take nutrients that would have been harvested by its other existing roots. If the plant can integrate these costs and benefits then it can curtail root production in response to intra-plant competition and achieve its highest yield when it has exclusive use over its space.

In response to inter-plant root competition, the marginal benefit of root production includes both new uptake and uptake that is at the expense of the other plant's uptake. As such the marginal benefit of root production is always higher in the face of inter-plant competition than intra-plant. But, as the other plant responds in kind, this benefit of additional roots becomes squandered and a tragedy of the commons becomes the expected ESS. Why must plants that can make a whole-plant decision engage in this over-production of roots? Because a plant that curtailed root production in response to inter-plant competition would be handing most of the collective benefits to the other plant that over-produced roots. To curtail root production in response to inter-plant competition is to pay a private cost (in terms of uptake) for a public benefit. Such a cooperative solution would require the plants to engage in some sort of reciprocal altruism or tit-for-tat.

The over-production of roots and the ensuing tragedy of the commons in response to inter-plant competition can help direct an understanding of patch use and habitat selection by plants. Hormones (auxin. cytokinins and gibberellic acid) influence the dynamics of root formation and growth. Specifically, the root tip is a source of a substance which moves basipetally and interacts with acropetally moving promoters which regulate root initiation. In addition, root tips produce a powerful inhibitor of lateral root emergence (Wightman & Thimann 1980). The hormones' movements may direct a higher root growth in a habitat of high nutrient availability. Under the assumption that the plant is behaving optimally, the overall objective would be to produce more roots in a manner that maximizes whole-plant fitness. The root-tip may perceive the presence of a neighboring competitor and send signals which regulate the flow of hormones. As this would occur in both plants, the plants would eventually engage in an arms race for more root production. Eventually, the plants would overproduce roots at the expense of other organ development. However, for the plant to maximize whole-plant fitness, the assessment and responses of individual growing tips must be coordinated with actions and consequences elsewhere in the plant. The plant goes from being a condominium of competing substructures to an integrated whole that is coordinated via non-cognitive behavioral responses to local hazards and opportunities.

It is not yet known which mechanism is responsible for the dependence of development of individual roots to the availability of nutrients in its own environment, and the influence of other roots of the same plant. Sachs et al. (1993) have suggested that this reorganization of plant growth may result from the activity of the cambium. The cambium enables the branches of the shoot and the root systems to collaborate and coordinate their growth. Cambium is also the basis for plasticity of vascular contacts, allowing for changes in the relations between organs as the plant develops and regulates resource allocation. Cambium activity may be regulated by hormones which could direct locally differential root expansion. Auxin could have a major role in such a competition serving as a measure of the developmental state of the roots and their environment (Novoplansky et al. 1989). The role of hormones may initiate more rapid growth by roots in better environments. In addition, the plant's hormones will assess the conditions and support growth in particular directions at the expense or inhibition of another organ.

The tragedy of the commons suggests ways of increasing crop yields. Yield can be enhanced by isolating plants from one another. By subdividing a space, the plants can produce higher yields for the same input of water and nutrients. This may not be practical for the cultivation of large fields of closely spaced plants. Alternatively, it should be possible to select for more 'docile' strategies of root allocation. Plants that curtail root production as much in response to others' roots as their own would contribute to maximizing collective yield. Of course, such a strategy is not evolutionarily stable in response to natural selection. But, specific forms of artificial selection in combination with more knowledge of the specific genetical and physiological mechanisms could produce novel strains of plants. Such plants could provide a commercial and an ecological win-win opportunity by either increasing yield for the same level of inputs of fertilizer and water, or the same yield for a reduced level of inputs.

The possibility of plants using a whole-plant strategy for distributing roots in response to intra- and inter-plant competition suggests several research directions. A question is opened regarding the specific mechanism by which root competition results in a tragedy of the commons and the mechanisms by which a plant assesses the whole-plant consequence of local root proliferation. Finally, plants through their root allocation may be as sophisticated in their habitat selection 'behavior' as animals. These responses may profoundly influence intra-specific competition. Also, this modeling and experimental approach can be applied profitably to inter-specific interaction with concomitant significance for plant communities. In summary, some of the great variety of responses noted in the literature for root competition may possibly be understood within the framework of whole-plant responses to nutrient foraging games.

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References

Ballare, C. L., Sanchez, R. A., Scopel, A. L. & Ghera, C. M. 1987. Early detection of neighbor plants by phytochrome perception of spectral changes in reflected sunlight. Plant Cell Environ. 10: 551–557.

Bazzaz, F. A. 1991. Habitat selection in plants. Am. Naturalist 137: S116–S130.

Brown J. S. 1998. Game theory and habitat selection. In: Dugatkin L. A. & Reeve, H. K. (eds), Game theory and animal behavior. Pp. 188–220. Oxford University Press.

Brown, J. S. and Rosenzweig, M. L. 1986. Habitat selection in slowly regenerating environments. J. Theor. Biol. 123: 151–171.

Campbell, B. D., Grime, J. P., Mackey, J. M. L. & Jalili, A. 1991. The quest for a mechanistic understanding of resource competition in plant communities: the role of experiments. Funct. Ecol. 5: 241–253.

D'Antonio, C. M. & Mahall, B. E. 1991. Root profiles and competition between the invasive, exotic perennial, *Carpobrotus edulis*, and two native shrub species in California coastal scrub. Am. J. Botany 78: 885–894.

Drew, M. C. & Saker, L. R. 1975. Nutrient supply and the growth of seminal root system in barley. II. Localized compensatory increase in lateral root growth and rates of nitrate uptake when nitrate supply is restricted to only one part of the root system. J. Exp. Botany 26: 79–90.

Fretwell, S. D. & Lucas, H. L. Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheor. 19: 16–36.

Gersani, M., Abramsky, Z. & Falik, O. 1998. Density-dependent habitat selection in plants. Evol. Ecol. 12: 223–234.

Gersani, M. & Sachs. T 1992. Development correlations between roots in heterogenous environments. Plant Cell Environ. 15: 463–469.

Gersani, M., Brown, J. S., O'Brien. E., Maina, G. G., & Abramsky, Z. 2001. Tragedy of the commons as a result of root competition. J. Ecol. 89: 661–669.

Hackett, C. 1972. A method of applying locality to roots under controlled conditions and the morphological effects of locally applied nitrate on the branching of wheat roots. Austral. J. Biol. Sci. 23: 1169–1180.

Hardin, G. 1968. The tragedy of the commons. Science 162: 1243–1248.

Hoagland, D. R. & Arnon, D. I. 1950. The water culture method for growing plants without soil. California Agricultural Experiment Station. Circular No. 374.

Mahall, B. E. & Callaway, R. M. 1991. Root communication among desert shrubs. Proc. Natl. Acad. Sci. USA 88: 874–876.

Mahall, B. E. & Callaway, R. M. 1992. Root communication mechanisms and intra-community distributions of two Mojave Desert shrubs. Ecology 73: 2145–2151.

McConnaughay, K. D. M. & Bazzaz, F. A. 1991. Is physical space a soil resource? Ecology 72: 94–103.

McConnaughay, K. D M. & Bazzaz, F. A. 1992. The Occupation and fragmentation of space: Consequences of neighboring roots. Funct. Ecol. 6: 704–710.

Morris, D. W. 1994. Habitat matching: Alternatives and implications to populations and communities. Evol. Ecol. 4: 387–406.

Novoplansky, A. & Cohen, D. 1997. The mutual distribution of competing root stems. Pp. 353–364 In: Altman & Waisel, (eds), Biology of Root Formation and Development. Plenum Press, New York.

Novoplansky, A., Cohen, D. & Sachs T. 1989. Ecological implications of correlative inhibition between plant shoots. Physiol. Plant. 77: 136–140.

Rosenzweig, M. L. 1991. Habitat selection and population interactions. Am. Natural. 137: S5–S28.

Rosenzweig, M. L. & Abramsky Z. 1985. Detecting density-dependent selection. Am. Natural. 126: 405–417.

Sachs, T., Novoplansky, A. & Cohen, D. 1993. Plants as competing populations of redundant organs. Plant Cell Environ. 16: 765–770.

Schenk, H. J., Callaway, R. M. & Mahall, B. E. 1991. Spatial root segregation: Are plants territorial? Advances in Ecological Research (in press).

Venable, D. L. & Brown, J. S. 1993. The population dynamic functions of seed dispersal. Vegetatio 107: 31–35.

Vincent, T. L., Van, M. V. & Goh, B. S. 1996. Ecological stability, evolutionary stability and the ESS maximum principle. Evol. Ecol. 10: 567–591.

Wightman, F. & Thimann, K. V. 1980. Hormonal factors controlling the initiation and development of lateral roots. I. Sources of primodal-inducing substances in the primary root of pea seedlings. Physiol. Plant. 49: 13–20.