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Tragedy of the commons as a result of root competition

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Summary

1 We develop and test a game-theoretic model for considering the effects of intra- and interplant competition on root proliferation and reproductive yield.
2 We predict that if space and resources per individual are held constant, plants should produce more roots per individual and less reproductive yield per individual as the number of plants sharing the combined space increases.
3 We tested the predictions using soybean plants (*Glycine max*) cultivated in the glasshouse either as owners or as two individuals sharing twice the space and nutrients.
4 Sharing individuals produced 85% more root mass than owners. Owners, however, produced 30% more reproductive yield per plant (dry mass of seeds), as a result of significantly more seed pods (8.70 vs. 7.66), more seeds per pod (1.87 vs. 1.72) and larger seeds (0.205 vs. 0.195 g seed^{-1}), than did sharing individuals.
5 Total plant biomass did not differ between owners and sharing individuals, but owners had significantly higher shoot to root ratios, produced significantly more seeds per unit root mass, and allocated a significantly higher percentage of total biomass production to seeds.
6 Possession of an evolutionarily stable strategy (ESS) of root competition suggests that different roots and parts of a plant assess and respond to opportunities in a manner that maximizes the good of the whole plant. Thus, plants may be more sophisticated and share more in common with animals in their non-cognitive behaviours than previously thought. A plant operating as a co-ordinated whole should, all else being equal, first proliferate roots in unoccupied soil, then in soil occupied by a conspecific competitor, and lastly in soil already occupied by its own roots.

Key-words: ESS, game theory, *Glycine max*, nutrient foraging, plant behaviour, root competition, soybeans, tragedy of the commons, legume

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Introduction

Plants adjust the proliferation, structure and physiology of their roots in response to resource availability and small-scale variation in nutrients, as well as to the presence of other roots (Campbell & Grime 1989; Friend *et al.* 1990; Campbell *et al.* 1991; De Kroon & Hutchings 1995; Gersani *et al.* 1998). All else being equal, plants proliferate roots preferentially in areas that are higher in nutrients and in areas free of other roots. Root segregation therefore occurs between individuals of the same species at scales ranging from millimetres up to metres, with the result that there is often little overlap between neighbouring root volumes (Nye & Tinker 1977). Among agricultural cultivars, root segregation has been documented for both soybeans (*Glycine max*) (Raper & Barber 1970) and onions (*Allium cepa*) (Baldwin & Tinker 1972).

Spatial segregation of plants gives a plant sole control over some part of the space it occupies (Brisson & Reynolds 1997; Casper & Jackson 1997). Root segregation has often been associated with architectural constraints (Cody 1986; Callaway 1990), spatial variation in nutrient supply, phenotypic plasticity, and allelopathy or non-toxic signals between roots (Mahall & Callaway 1991, 1992). Root competition and segregation may be analysed using game theory in that the optimal root allocation of an individual may be strongly influenced by the root proliferation strategies of other plants. Here, we consider intraspecific root proliferation as a game of nutrient foraging.

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We develop a game theory model of root proliferation when the plant shares its space with varying numbers of competitors. The model predicts the evolutionarily stable strategy (ESS, Maynard Smith & Price 1973) level of root production. The ESS is optimal in the sense that the individual cannot improve its fitness by unilaterally changing its strategy. It is not necessarily optimal in the sense of maximizing the collective fitness of all plants sharing the same space. In fact, the model predicts that interplant root competition will result in a tragedy of the commons (Hardin 1968). A tragedy of the commons occurs whenever an individual gains at the expense of others. The private gain to an individual from increasing its root growth is smaller than the public cost to others. If root competition occurs in accord with the model, then each of two plants sharing a common space should produce more roots but have a lower reproductive yield than if they enjoyed exclusive use of half the space.

We tested the model's predictions with soybeans. We planted two split-root seedlings either separately in their own pot (providing two **owners** with exclusive access to half of the total space), or as pairs of individuals both straddling two pots (providing two individuals with **shared** access to the entire space). We also grew seedlings in boxes that were either intact (sharing) or divided into two exclusive compartments (owners). We then allowed the plants to grow to maturity, at which time we measured root mass, seed production, and above ground production of leaves and stems.

Model and research objectives

A fitness generating function (G-function, *sensu* Brown & Vincent 1987; Vincent *et al*. 1993) can be used in evolutionary games to describe the expected success of an individual as influenced by its own characteristics (here, root proliferation) and those of others. We will use a simple model of root proliferation by annual plants to consider how intra- vs. interplant root competition influences a plant's ESS level of root proliferation and its subsequent reproductive yield. In the following model, as the number of plants sharing the same space increases from one to many, plants shift from experiencing primarily intraplant root competition to experiencing primarily interplant root competition.

Let N individual plants share the same soil space. Let total nutrient uptake be a decelerating function of the total root production of all of the plants, and let each individual's share of nutrient uptake be in proportion to its own root biomass relative to the root biomass of others. Under these assumptions, nutrient competition is exploitative, and total nutrient harvest increases with total root mass but at a diminishing rate that eventually asymptotes at the total amount of available nutrients. Let fitness be determined by the difference between an individual's nutrient uptake and the cost of growing, maintaining and servicing its roots (this cost subsumes in units of nutrients the associated above ground plant parts needed for photosynthesis, seed production and root maintenance). We also assume that above ground competition is negligible or constant within the range of considered root production strategies.

The fitness generating function, by combining the above assumptions, determines the net nutrient profit of an individual plant as a function of its own root production and that of others. This fitness generating function will be frequency- and density-dependent according to the following:

$$G(u,u,N) = (u/x)H(x) - C(u) \qquad \text{eqn 1}$$

where u is the root production of the focal individual, x (calculated as $u + \Sigma u_i$) is the total of all individuals' root production, u is the vector of root production among the other $N - 1$ individuals, $H(x)$ is total nutrient uptake as a function of total root production, and $C(u)$ is the cost to the individual of supporting its roots and associated above ground parts. Notice that u changes as the focal individual changes.

Although our experiments use root mass to measure nutrient foraging effort, the rooting strategies represented by u and x can reflect changes in other characters that increase nutrient uptake at a cost, such as increases in fine root density, total root surface area (Fitter *et al*. 1991), or root kinetics (Drew & Saker 1975; Lee 1982; Jackson *et al*. 1990). For a single rooting strategy, u^*, to be an ESS it must satisfy the ESS maximum principle (Vincent *et al.* 1996). It must maximize G with respect to u when both the focal individual and colleagues are using the same strategy: all elements of u equal u^*. To seek a strategy, u^*, that is an ESS, we calculate the fitness gradient with respect to u:

$$\partial G/\partial u = H(x)[x - u]/x^2 + (u/x)\partial H/\partial x - \partial C/\partial u, \qquad \text{eqn 2}$$

set the gradient equal to zero (for an interior solution), and evaluate at $u = u = u^*$. Thus, the ESS root production of the individual satisfies:

$$\frac{(N-1)}{N} \cdot \frac{H(x)}{x} + \frac{1}{N} \cdot \frac{\partial H}{\partial x} = \frac{\partial C}{\partial u} \qquad \text{eqn 3}$$

Equation 3 is general and shows that the individual plant generates an optimal production of roots by weighting the average and marginal values ($H(x)/x$ and $\partial H/\partial x$, respectively) of producing roots, with the weighting dependent upon the number of competitors, N. As N increases, the individual plant weights its decision more heavily towards its average return per unit root and less on its marginal return per unit root. Therefore, at $N = 1$ (no interplant competition), the plant bases root production entirely on the marginal benefit but, as $N \to \infty$, its decision is based entirely on the average reward.

We assume however, that resources (nutrients and space) per individual remain constant as the number of individuals increases. Consider, for example the following three scenarios in the commons: (i) $N = 10$, where all 10 individuals share the same space, (ii) $N = 2$, where the space is subdivided into pairs of individuals to create 5 equally sized soil compartments, and (iii) $N = 1$ (10 compartments, each with one individual). Assuming that nutrient uptake is through exploitative competition and that each individual within a compartment has equal access to the resources of the compartment (we are ignoring distance effects created by the exact spatial arrangement of plants), the following relationships hold true for the rates of total nutrient uptake, marginal nutrient uptake, and average nutrient uptake, respectively:

$$H(x) = 10H(x/10)_{N=1} = 5H(x/5)_{N=2} = H(x)_{N=10} \quad \text{eqn 4a}$$

$$\partial H/\partial x = \partial H(\text{x}/10)_{N=1}/\partial x = \partial H(x/5)_{N=2}/\partial x = \partial H(x)_{N=10}/\partial x \quad \text{eqn 4b}$$

$$H(x)/x = 10H(x/10)_{N=1}/x = 5H(x/5)_{N=2}/x = H(x)_{N=10}/x \quad \text{eqn 4 c}$$

The subscripts refer to the number of individuals sharing a compartment and the first, second and third terms of each expression therefore describe the particular uptake rate in the commons summed across ten, five and one compartments, respectively. We can determine the ESS root production per individual for each scenario (i.e. for the various sized commons) by substituting the appropriate value for N into equation 3:

$N = 1$ (10 individuals in 10 subdivided spaces):

$$\frac{\partial H}{\partial x} = \frac{\partial C}{\partial u} \quad \text{eqn 5a}$$

$N = 2$ (10 individuals in five subdivided spaces):

$$0.5\frac{H(x)}{x} + 0.5\frac{\partial H}{\partial x} = \frac{\partial C}{\partial u} \quad \text{eqn 5b}$$

$N = 10$ (10 individuals share the entire, undivided, space):

$$0.9\frac{H(x)}{x} + 0.1\frac{\partial H}{\partial x} = \frac{\partial C}{\partial u} \quad \text{eqn 5c}$$

These equations (5a–c) show how the ESS of several plants sharing the same space results in a tragedy of the commons (Hardin 1968). When $N = 1$ and the individual ‘owns’ its space, the individual produces roots until the marginal reward from additional roots ($\partial H/\partial x$) no longer exceeds the marginal cost ($\partial C/\partial u$). This maximizes both individual and collective fitness. As N increases, ESS root production represents a weighted averaging of the marginal reward and the average reward (H/x) of root production relative to the marginal cost. In fact, as N goes to infinity the plant produces roots until the average benefit no longer exceeds the marginal cost. For a decelerating curve that goes through the origin (as assumed for $H(x)$), the average of the curve will always be greater than the margin: $H/x > \partial H/\partial x$ (Fig. 1a). Hence, 10 plants sharing the commons ($N = 10$) will produce more roots per individual, than five pairs of plants ($N = 2$) spread over five subdivisions of the commons, and the five pairs of individuals will produce more roots per individual than 10 individuals each with its own subdivided space of the commons ($N = 1$): $x^*_{N=10} > x^*_{N=2} > x^*_{N=1}$, where x^* refers to total root production across the entire space (for this example, root production per individual, u^*, is found by dividing x^* by 10) (Fig. 1b). Reproductive yield is maximized at $x^*_{N=1}$, as can be shown by simply maximizing total nutrient profits, $NG(u,\underline{u},N)$, with respect to total root production. The condition for maximizing collective reproductive yield reduces to equation 5a. The owners ($N = 1$) will therefore produce more reproductive yield per individual than the five pairs of individuals ($N = 2$), which will produce more reproductive yield per individual than the

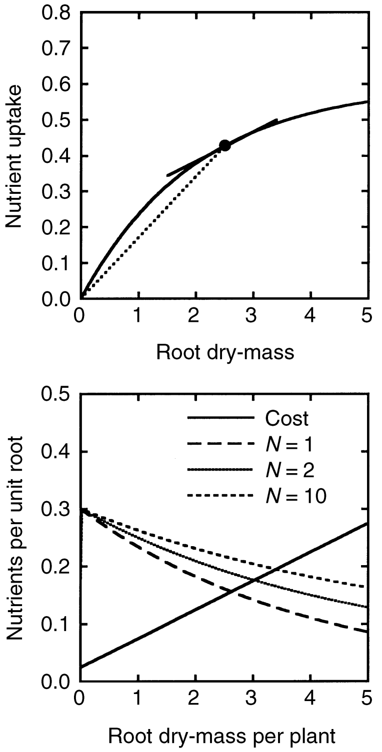

Fig. 1 (a) The assumed relationship between nutrient uptake and root proliferation. Because the curve is decelerating and passes through the origin, the average rate of nutrient harvest per unit root (the slope of the dotted line) is always greater than the marginal rate of nutrient harvest per unit root mass (the slope of the solid tangent line). The point on the curve is arbitrary for purposes of illustration. (b) The ESS root proliferation for each of 10 individuals sharing a common space ($N = 10$), two individuals ($N = 2$) sharing a space that is one fifth the size of the space with 10 plants, and one individual ($N = 1$) possessing its own space that is one tenth the size of the space with the 10 plants. The ESS root allocation is the intersection of the appropriate negatively sloped benefit curve and the positively sloped marginal cost curve. The cost curve will have positive or negative slopes if per unit cost of roots increases or decreases, respectively, with root production.

10 individuals sharing the commons ($N = 10$): $G(u^*_{N=1},u^*_{N=1},10) > G(u^*_{N=2},u^*_{N=2},10) > G(u^*_{N=10},u^*_{N=10},10)$.

Why do individuals sharing space over-produce roots and sacrifice collective reproductive yield at the ESS? The fitness generating function is frequency-dependent in that an individual's best strategy depends upon the root allocation of other plants sharing the same space. The presence of competitors and the opportunity to 'steal' nutrients from others encourages the plant to produce more roots over and above those which would maximize collective gains. By producing more roots, the individual enhances its own reproductive yield at the expense of others. However, as the other individuals respond in kind, the advantage is lost.

Evolutionary game theory can thus be applied to a simple model of root competition (see Brown 1998 for an example of a similar model in the context of animal ecology and density-dependent habitat selection). Annual plants competing exploitatively for nutrients will be expected to engage in a tragedy of the commons and over-produce roots relative to the level which would maximize collective reproductive yield. This depends on an ability to differentiate between 'self' vs. 'others' when regulating root production in response to competition and also suggests that selective breeding may be needed to avoid this loss of reproductive yield in the roots of crop plants if we have not recognized this propensity in cultivars.

We chose soybeans (*Glycine max* L.) for an initial test of the theory because they have large seeds, respond well to the split-root techniques used, have a fixed timing of seed maturation, and produce roots, shoots and fruit that are easy to collect and quantify from glasshouse cultivated plants. As nodulating legumes, soybeans may contribute some additional nitrogen to the system in contrast to non-leguminous forbs.

The specific objectives of this study include determining:

1. Does soybean engage in a tragedy of the commons via root competition?

Prediction 1: If soybean allocate their roots in accord with the model then owners (plants with exclusive use of their space) should produce less root mass and more reproductive yield per individual than sharing individuals.

2. Do the owners vs. sharing individuals allocate biomass differently between roots and shoots?

Prediction 2: While we cannot predict how total shoot biomass will differ between treatments, we expect that owners will have the higher shoot to root ratio.

3. Does the cultivation technique for comparing owners and sharing individuals influence the tragedy of the commons? In one set of experiments, sharing individuals were generated by having split-root plants straddling pairs of pots, while owners were represented by a single plant occupying its own pot. We did not want results to be an artefact of experimental techniques relating to the split-root technique, the initial proximity of competitors' roots, and the means for dividing space between individuals. In a separate experiment, plants were grown in boxes which contained two plants that either had no soil-divider (sharing individuals) or a divider that separated the plants (owners). In the split-root pot experiment, the roots of sharing individuals were initially in close proximity, whereas in the boxes they were well separated.

Prediction 3: Although overall reproductive yield and shoot to root ratios may differ, the cultivation techniques used should not alter the prediction that owners will have higher reproductive yield, while producing less roots, and exhibiting higher shoot to root ratios.

Methods

During the winter of 1998, soybean plants (*Glycine max* William's variety, from University of Illinois, Urbana) were grown in a heated glasshouse (21–27 °C) at the University of Illinois at Chicago. Plants were grown under ambient light conditions, supplemented by artificial light (a combination of fluorescent white lamps and high pressure sodium lamps) of about 1400 μ-Einsteins during a 14-h photoperiod.

SPLIT-ROOT PLANTS GROWN IN POTS

To create split-root individuals we followed the technique of Gersani *et al.* (1998). After soaking for 24 h in aerated water, seeds were sown in potting soil for another 24 h. Once a radicle had emerged, the distal 1–1.5 mm of root tip was removed and the seedling replanted, with the radicle pointing down, for a further 5 days. Two approximately identical roots that had grown from the cut surface were kept, thus creating a split-root seedling, and all other roots (including lateral roots) were removed before the seedlings were transplanted into pots (25 cm high × 26 cm diameter) filled with vermiculite.

To create sharing individuals (Fig. 2a), two plants were planted in two adjacent pots with each plant having one root in each pot. To create owners (Fig. 2a), we planted two plants in two adjacent pots, but this time, both roots of a split-root seedling were planted in a single exclusive pot. Under both treatments, seedlings were planted in close proximity to each other at the interface between adjacent pots. While each root had another root in close proximity, the neighbouring root was from another plant (interplant competition) for the sharing treatment, and from the same plant (intraplant competition) for the owner treatment. Pairs of pots were arranged on benches as blocks of four pairs (two pairs of sharing individuals and two pairs of owners). Furthermore, four blocks were arranged on each of two benches for a total of eight blocks and 32 pairs of pots. Using a drip irrigation system, each pot was saturated with 400 mL of 10% strength Hoagland's solution every second day. Excess solution drained through holes in the base of the pots. To prevent any mineral salt accumulation in the vermiculite, we used 400 mL of distilled water every fourth watering.

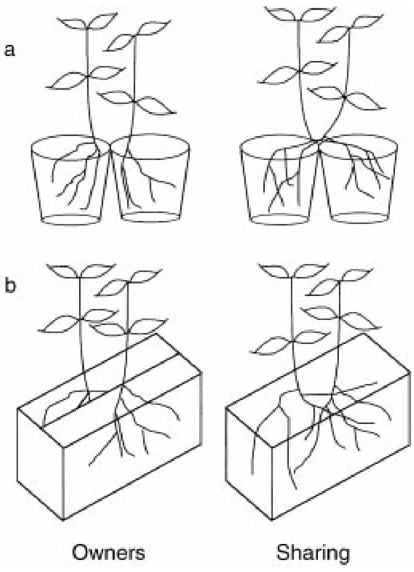

Fig. 2 The experimental planting to create owners (no interplant root competition) and sharing individuals (with interplant root competition): (a) split-root seedlings within pairs of pots and (b) in boxes. In both cases we expect the owners to produce fewer roots and more seeds per individual.

After pods and seeds had ripened, plants were harvested on 29 April 1999 (*c.* 110 days of growth). We separated the roots from the vermiculite of each pot, and the pods, seeds, leaves, and stem from each plant. Plant material was oven dried at 70 °C for three days. Following drying, we measured dry weight of pods, seeds, leaves, stems, and roots. Above ground production could be assigned to an individual plant. In the treatment with sharing individuals, roots were assigned to a pot and not to an individual.

PLANTS GROWN IN BOXES

Seeds of soybeans were sown in wooden boxes that were either undivided (50 × 20 × 26 cm high) or subdivided into two compartments of equal size (50 × 10 × 26 cm high). The interior of the box of each chamber was covered with thick plastic containing drainage holes. Each box was filled with a mixture of silica sand and vermiculite in a 1 : 1 ratio by initial dry volume. The sharing treatment (Fig. 2b) involved planting two plants in the middle of each of the undivided boxes at a distance of 10 cm from each other. The owner treatment (Fig. 2b) involved planting one plant in the middle of each of the two compartments of the subdivided boxes, with the base of each plant *c.* 10 cm from the other. The average amount of space per individual was the same under the sharing and owner treatments.

The boxes were watered with a similar irrigation system as that used for the split-root plants in the pots. However, after the first 4 weeks, we used a 0.1 Hoagland's solution that lacked nitrogen: 0.005 M $Ca(H_2PO_4)_2$, 0.05 M K_2SO_4, 0.001 M $CaSO_4$, 0.1 M $MgSO_4$, Iron EDTA, trace nutrient solution. On 22 April 1999, after *c.* 110 days, the plants were harvested. Roots, pods, seeds, leaves and stem were collected, dried and weighed.

ANALYSIS

We used a partially hierarchical MANOVA (Brownlee 1965) to test for the effects of planting treatment (sharing vs. owners) and cultivation technique (pots vs. boxes) on seed production, root mass, shoot mass, and total plant biomass. Pod mass, seed mass, root mass, and shoot mass data were log-transformed to normalize the data and to linearize the geometric growth processes of plants. We then averaged the data for pairs of pots. While this reduces the sample size from 256 plants to 128 pairs, it removes the problem created by our inability to assign roots to individuals in the sharing treatment. In the analysis, blocks represent a random effect nested within cultivation technique. We used ANCOVAs to test for the effect of planting treatment (owner vs. sharing) and cultivation technique (pots vs. boxes) on the amount of seeds as a function of root mass and on the amount of shoot as a function of root mass. In these analyses, seed mass or shoot mass (average from a pair) was the dependent variable, planting treatment and cultivation technique were the group factor, and root mass (average from a pair) was the covariate.

Results

In accord with prediction 1, owners produced significantly more reproductive yield (measured as dry mass of seeds) and significantly less root biomass than sharing individuals (Fig. 3). Per individual plant, reproductive yield was *c.* 30% higher ($F_{1,61} = 11.6$, $P < 0.005$) and mean root mass per individual plant was *c.* 46% lower ($F_{1,61} = 22.1$, $P < 0.001$) for owners than for sharing individuals, but shoot mass (stem plus leaves) did not differ ($F_{1,61} = 0.52$, n.s.).

Both root mass and reproductive yield were higher in box-grown soybeans than in pots (*c.* 90% and 35%, respectively, $F_{1,61} = 15.1$, $P < 0.001$), but shoot mass did not differ ($F_{1,61} = 0.02$, n.s.). In accord with prediction 3, cultivation technique (boxes vs. split-root plants in pots) did not influence the effect of sharing vs. owner, nor was there a significant interaction between cultivation technique and competition treatment. The model's predictions were robust despite differences in nutrient regime (reduced nitrogen in boxes) and cultivation protocol.

A soybean plant can increase its reproductive yield by increasing: (i) the number of pods, (ii) the number of seeds per pod, or (iii) the mass of each individual seed (presuming that large seeds have an advantage over small seeds). Owners significantly outperformed sharing individuals in all measures of reproductive yield (8.70 vs. 7.66 pods plant^{-1}, $F_{1,61} = 4.01$, $P < 0.05$, 1.87 vs. 1.72 seeds pod^{-1}, $F_{1,61} = 7.94$, $P < 0.01$, 0.205 vs. 0.195 g seed^{-1}, $F_{1,61} = 6.56$, $P < 0.02$).

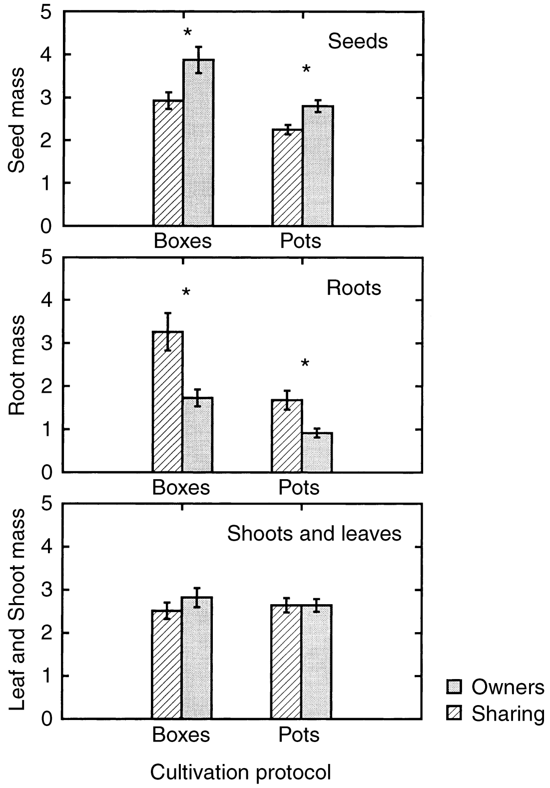

Fig. 3 Average seed, root, and shoot (stems plus leaves) production of soybeans grown in either the boxes or the pots as either owners or sharing individuals. All values are per individual and graphed in units of grams of dry mass. The error bars indicate one standard error above and below the mean. The asterisks indicate significant differences between owners and sharing individuals.

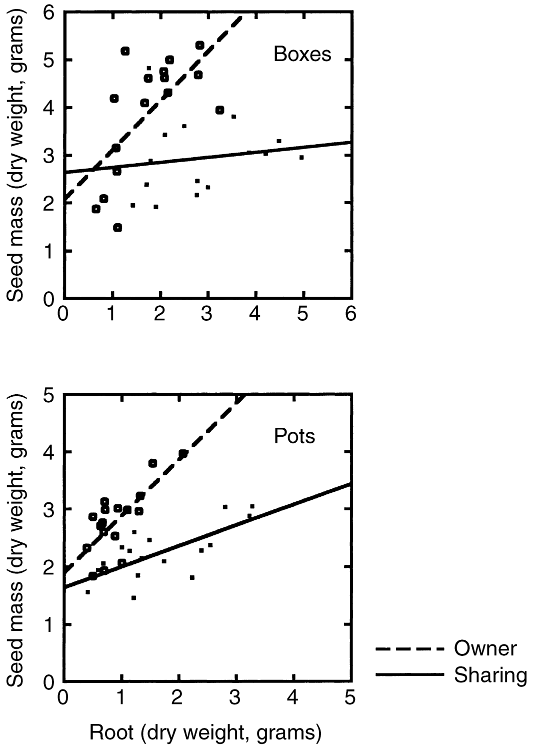

Fig. 4 The relationship between seed and root production in the boxes and pots.

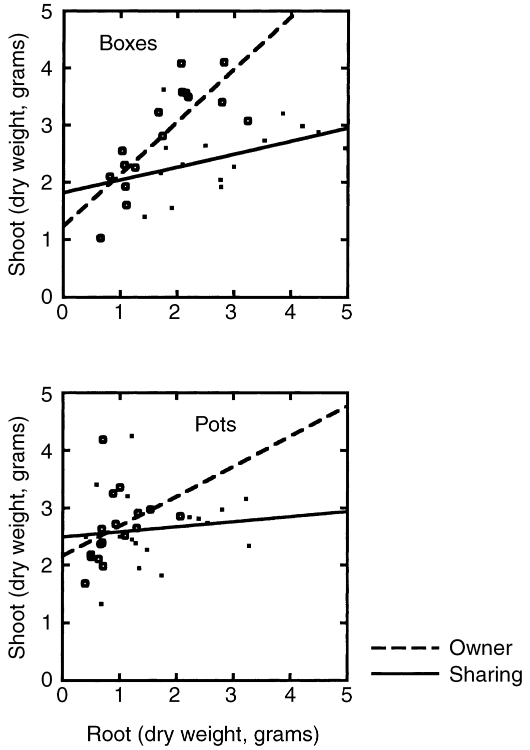

Fig. 5 The relationship between shoot (stem plus leaves) and root production in the boxes and pots.

Cultivation technique significantly influenced two of the three measures of reproductive yield. Plants grown in the boxes (relative to split-root plants in pots) produced significantly more pods (9.06 vs. 7.38, $F_{1,61} = 10.51$, $P < 0.002$) and significantly more seeds per pod (1.86 vs. 1.74, $F_{1,61} = 4.87$, $P < 0.05$) but the size of seeds did not differ (0.204 vs. 0.197 g seed^{-1}, $F_{1,61} = 3.35$, n.s.).

Owners and sharing individuals differed significantly in their allocation of biomass to roots, shoots and reproductive yield (Figs 4 and 5). The ANCOVA with reproductive yield as the dependent variable revealed a significant positive relationship with root mass as the covariate ($F_{1,59} = 48.4$, $P < 0.001$) although intercepts did not differ ($\bar{x} = 1.87$ g, $F_{1,59} = 0.40$, n.s.), owners had a significantly higher slope (1.04 vs. 0.69, $F_{1,59} = 17.5$, $P < 0.001$). Hence, within either planting treatment, increased root mass is associated with increased reproductive yield, but owners achieve a higher reproductive yield per unit root mass than sharing individuals (Fig. 4). Cultivation technique (boxes vs. pots) did not significantly influence either the intercept ($F_{1,59} = 0.67$, n.s.) or the slope ($F_{1,59} = 0.05$, n.s.) of the relationship between reproductive yield and root mass.

The ANCOVA with shoot mass as the dependent variable also yielded a significant positive relationship with root mass (as the covariate, Fig. 5) for both treatments, with similar intercepts (1.78 g; $F_{1,59} = 1.7$, n.s.), but a significantly higher slope for owners (slopes of 0.82 vs. 0.52; $F_{1,59} = 14.9$, $P < 0.001$). Hence, owners had a higher shoot : root ratio than sharing individuals.

With respect to cultivation technique, plants in boxes (relative to pots) had a significantly lower intercept ($F_{1,59} = 9.7$, $P < 0.005$), but no significant difference in slope ($F_{1,59} = 2.30$, n.s.). This result, combined with the higher average root mass of plants in boxes, shows that boxes produced plants with a lower shoot : root ratio than the split-root plants grown in pots.

Discussion

The results show that root competition between soybean plants results in a tragedy of the commons (*sensu* Hardin 1968). The plants responded to their competitive environment in a manner consistent with our game theory model of intra- vs. interplant root competition. Plants curtailed root production when their own roots represented the sum of the competitive environment (owners) and exaggerated root production in the presence of others' roots (sharing individuals). Hence, when a seedling owned its space, it produced significantly more fruit and less root compared to a plant that shared its space with another plant, despite there being a constant amount of space and nutrients per individual across planting treatments (owners vs. sharing).

The tragedy of the commons was manifest across two different forms of cultivation. The technique of creating split-root seedlings and cultivating these plants in pots led to reductions in both growth and reproductive yield when compared with intact seedlings grown in boxes. The split-root treatment may have heightened interplant root competition between sharing individuals since the roots of sharing individuals started the experiment much closer together (1 cm vs. 10 cm in boxes). However, despite the 10-fold difference in plant spacing between cultivation treatments, the proportional increases in reproductive yield and reductions in root mass between owners and sharing individuals were remarkably similar.

Total biomass (root mass + shoot mass + total mass of pods and seeds) did not differ between owners and sharing individuals; but owners allocated proportionally more to reproductive yield and to shoots, and sharing individuals allocated proportionally more to roots. If the rate of carbohydrate production is similar at each developmental stage, then overproduction of roots by the sharing individuals must come at the expense of other tissues; in this case, seeds. Owners produced more pods and more seeds per pod, as well as larger seeds which may influence trade-offs between offspring quality and offspring number (Smith & Fretwell 1974).

Calculations of seed production vs. root production suggest that the owners showed (i) higher rates of nutrient uptake per unit root, and (ii) a steeper relationship between root mass and total nutrient uptake than did sharing individuals. Owners may thus acquire significant amounts of nutrients by producing additional roots (relatively high marginal value of roots), whereas sharing individuals benefit much less from root proliferation (relatively low marginal value of roots).

MODELS OF ROOT PRODUCTION UNDER COMPETITION

Few models make explicit predictions regarding how plants should adjust root production in response to intra- vs. interplant competition. Models based on an ideal free distribution (Fretwell & Lucas 1970) of root mass or passive habitat selection based on reinvesting net profits predict no difference in root proliferation or reproductive yield between owner or sharing individuals. Our model is an extension of the root proliferation model of Gleeson & Fry (1997), which considers just a single plant, to include any number of conspecific competitors sharing the same space. The model of Novoplansky & Cohen (1997), which considers root competition as a two-player game in a spatial context (it is a variant of an R* model, Tilman 1988), predicts little to no spatial overlap between the roots of adjacent individuals. In our experiments the roots of sharing individuals were encouraged to intermingle and, indeed, visual inspection revealed complete intertwining of the roots of sharing individuals.

One alternative explanation for the sharing individuals producing more roots and less reproductive yield is that space itself is a resource in addition to the nutrients and water it provides (McConnaughay & Bazzaz 1991, 1992). It is possible that sharing individuals were responding to the additional space independent of the presence of their neighbours or of nutrient availability: so that more space results in the production of more roots. While this remains a possibility, we do not favour this explanation: the sharing individuals should not only produce more roots but should also benefit from this increased resource in terms of increased rather than decreased reproductive yield. This was not the case; sharing individuals produced less reproductive yield suggesting that space is not a resource for this species.

The overproduction of roots by sharing individuals in response to interplant competition contradicts simple models of nutrient foraging, whereby the presence of a competitor's roots would be expected to reduce nutrient availability and thus retard root production. Our model and results challenge the expectation of root allocation based on passive habitat selection or from an ideal free distribution of roots, which are based on statements such as: 'It is generally agreed that individual sink organs control carbohydrate partitioning by competing with one another based upon their sink demand and the relative ability of the translocation system to deliver carbohydrates to them' (Grossman & DeJong 1995). By engaging in a two-player game of root competition with its neighbour, the plant exhibits some integration at the level of the whole plant (Brown 1998), allowing a co-ordinated response by the individual plant to its competitive environment. Rather than viewing the plant parts as selfishly controlling the whole (Wardlaw 1990; Farrar 1993), our results suggest that the parts act in an integrated fashion for the good of the whole plant.

A limitation of our current model is the lack of spatial considerations. In Novoplansky & Cohen's (1997) model, for instance, the spatial component gives plants a competitive advantage in spaces closer to themselves than to their competitor. As the number of competing plants increases, or as the amount of space shared between them increases, an explicit consideration of space may become essential for predicting root production in response to interplant competition and to spatial proximity of nutrients. Our model could be extended to include spatial proximity by letting root uptake kinetics or the costs of roots change with distance from the plant. The game of nutrient foraging would become asymmetric in space, yet the same concepts of our model would still apply. This richer scenario with its potential for richer predictions awaits further work.

NON-COGNITIVE BEHAVIOUR IN PLANTS

How do our plants exaggerate or curtail root production in response to inter- vs. intraplant competition? Plant individuals may assess each other in several ways. When a plant competes with its neighbour, it benefits from 'defending' space and the nutrients contained therein, possibly with individual plants interacting directly with resources and only indirectly with each other. The most efficient way for a plant to compete with its neighbour may be to take the resource before its neighbour does and such indirect root interactions may favour speed over efficiency of nutrient uptake (D'Antonio & Mahall 1991; Nobel 1997).

In addition to competition through resource depletion, contest competition may occur where the roots of different individuals may interact directly by releasing organic compounds that diffuse through the soil. Compounds may include toxic exudates that inhibit the growth and development of neighbouring plants (e.g. allelopathy, Williamson 1990; Inderjit *et al.* 1995) as well as non-toxic signals that indicate an individual's presence (Aphalo & Ballare 1995; Bruin *et al.* 1995). Such direct interactions may allow assessment of the origin of neighbouring roots (as self or non-self). Schenk *et al.* (1999) expect such responses to ensure that root systems of different plants show a high degree of segregation. Ownership of space allows a plant to favour efficiency rather than speed of uptake when developing its root mass, architecture, and uptake kinetics. In addition to simply growing more roots as a means of increasing the speed of nutrient uptake, plants could also engage in the tragedy of the commons through increased root kinematics (BassiriRad & Caldwell 1992; Gersani *et al.* 1993), redistribution of root architecture to costlier morphologies (Gersani & Sachs 1992), and other more costly but speedier uptake mechanisms.

TRAGEDY OF THE COMMONS FROM INTERPLANT COMPETITION

We have little understanding of how a plant may assess neighbouring roots to generate a whole-plant allocation response. The over-production of roots by our sharing individuals and the complete overlap and intermingling of root systems suggest that the soybeans engaged in exploitation (or scramble) competition rather than contest (or interference) competition. The sharing individuals were unable to accommodate each other with respect to space. In the pots, the sharing individuals did not divide the space by 'giving' one pot to each plant (as the owners were forced to do). Similarly, in the boxes, sharing individuals did not constrain their root proliferation to the areas closest to themselves while ceding space closer to the other individual (as the dividers forced the owners to do). Such division of space in either experiment would have allowed the pair of plants to increase their reproductive yield.

The failure of the plants to 'co-operate' follows the expectation of the Prisoner's Dilemma (Axelrod & Hamilton 1981). If one of the plants 'co-operates' by ceding space and proliferating roots in just one compartment or area, it will lose, as the other plant enjoys both its exclusive space and proliferates into the space of its partner. In our model of root competition between pairs of individuals, highest reproductive yield goes to the individual that over-produces roots in the face of a partner that restrains root production. Next highest reproductive yield occurs when each partner restrains root production (as in the case of our owners). This reproductive yield is followed in rank order by partners that both overproduce roots (the present case of our sharing individuals). Lowest reproductive yield accrues to the individual that restrains root production against a competitor that over-produces roots.

The tragedy of the commons exhibited by the plants competing for nutrients is like that exhibited by plants competing for light (Gadgil & Gadgil 1975; Vincent & Brown 1984; Schieving & Poorter 1999). Short plants provide an efficient means for maximizing net profit from intercepting sunlight. However, an individual is under selection to produce a taller stem or trunk as a means of intercepting more sunlight by 'stealing' light from its neighbours. Once the other plants respond in kind, the benefits of additional height are negated and the population of plants now pays a larger price for supporting the additional stems and trunks. Wood and tree trunks may be the most conspicuous manifestation of foraging games among plants (Givnish 1982; Oksanen 1990).

Conclusions

Game theory can provide a useful modelling tool for understanding nutrient foraging under intra- and interplant competition. Under purely exploitative competition, interplant competition for a shared space should result in an over-proliferation of roots at the expense of collective reproductive yield relative to that of plants that have exclusive use of space. This model of whole plant response to foraging opportunities should apply beyond plants to animals such as ants, social bees and other social species that share food as a colony (Brown 1998). The ESS root allocation should influence intra- and interspecific competitive interactions between plants (Ryser & Lambers 1995). Finally, plants through their root allocation patterns may be as sophisticated in their habitat selection 'behaviours' as animals, and these responses may have as profound an influence on plant communities as they have been shown to have for animal communities (Bazzaz 1991; Rosenzweig 1991).

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