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Evolutionarily stable strategies for nutrient foraging and below-ground competition in plants

Gordon G. McNickle and Joel S. Brown

Department of Biological Sciences, University of Illinois at Chicago, Chicago, Illinois, USA

ABSTRACT

Question: How do differences in uptake kinetics caused by varying conditions of interspecific competition influence the evolutionarily stable root production strategies of plants?

Mathematical method: We present a game-theoretic model that investigates trade-offs between efficient nutrient harvest and neighbour pre-emption as evolutionarily stable strategies. The model builds upon previous game-theoretic models by incorporating potential differences in uptake capacity among competing plants, and by extending the model to interspecific competition.

Key assumptions: We assume that plants exhibit plasticity in growth that is informed by cues in the environment. We also assume that soil resources are limiting while light is not limiting to plant growth, and root costs increase linearly with root biomass. Finally, we assume a spatially implicit soil environment with infinite mixing of nutrients.

Conclusions: The model predicts plants should invest primarily in efficient nutrient harvest when soil fertility is low, per-root costs are high or uptake ability is low. Under these conditions, the plants produce fewer roots when neighbours are present compared with when grown alone. Alternatively, when soil fertility is high, per-root costs are low or uptake ability is high, the plants should invest heavily in more roots than are necessary to harvest available nutrients, thus pre-empting their neighbours. Under these conditions, the plants produce more roots compared with when grown alone.

Keywords: asymmetric game, best response curve, evolutionarily stable strategies, evolutionary game theory, interspecific competition, plant–plant competition, root games.

INTRODUCTION

Plants compete for nutrients in soil with their roots. This below-ground competition can often be more intense than above-ground competition and reduce plant performance by more than an order of magnitude (Wilson, 1988; Casper and Jackson, 1997; Schenk, 2006; Lamb and Cahill, 2008). Competitive effects are also often variable among species, leading to variable conditions of competitive intensity (Keddy *et al.*, 1994; Goldberg *et al.*, 1999; Thorpe *et al.*, 2011). The strong negative effects of root competition, and variable root allocation strategies among species, mean that

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Correspondence: G.G. McNickle, Department of Biological Sciences, University of Illinois at Chicago, 845 W. Taylor St. (MC066), Chicago, IL 60607, USA. e-mail: mcnickle@uic.edu

plants should be under considerable selective pressure to assess and respond to their competitive environment (Givnish, 1982; Gersani *et al.*, 2001; Falster and Westoby, 2003; Craine, 2006; Cahill *et al.*, 2010; Cahill and McNickle, 2011; Dybzinski *et al.*, 2011). Indeed, although the cues remain largely unknown, plants appear to be capable of sensing the presence of neighbour roots (Falik *et al.*, 2003, 2011; Gruntman and Novoplansky, 2004; Novoplansky, 2009) and many plants adjust patterns of allocation in the presence of specific neighbours and specific environmental cues (Maina *et al.*, 2002; Cahill *et al.*, 2010; Mommer *et al.*, 2010; Semchenko *et al.*, 2010; Cahill and McNickle, 2011).

Although we know that plants can, and often do, respond to neighbour roots, there is still little consensus concerning the optimal allocation strategies for below-ground competition, and how (or in many cases even whether) adaptively foraging plants should respond to cues from neighbours (Craine *et al.*, 2005; Schenk, 2006; Hess and de Kroon, 2007; Novoplansky, 2009; Herben and Novoplansky, 2010; Cahill and McNickle, 2011; de Kroon *et al.*, 2012). At the heart of this controversy is the question of whether it is adaptive for plants to respond only indirectly to neighbours solely through changes in resource levels (Grime, 1979; Tilman, 1982; Hess and de Kroon, 2007; de Kroon *et al.*, 2009), or whether it is adaptive for plants to respond to both resource levels and the competitive strategies employed by neighbours (Gersani *et al.*, 2001; Craine *et al.*, 2005; Craine, 2006; O'Brien *et al.*, 2007; O'Brien and Brown, 2008; Murphy and Dudley, 2009; Bhatt *et al.*, 2011; Cahill and McNickle, 2011). This is an ongoing debate and data are still mixed, but predictive theory is needed to generate testable hypotheses that can drive this field forward. Here, we analyse a model based on the assumption that plants are capable of assessing and responding to cues from neighbours. Our goal is not to conclude that plants do respond to cues from neighbours, but rather to ask 'if plants do respond to neighbours, what is their best strategy?'. We seek to expand the tool-kit of testable hypotheses available to plant ecologists and address some past criticisms and shortcomings of previous game-theoretic models of root competition (Laird and Aarssen, 2005; Schenk, 2006; Hess and de Kroon, 2007).

Previous game-theoretic models for plastic root strategies (Gersani *et al.*, 2001; O'Brien *et al.*, 2007; O'Brien and Brown, 2008) differed from empirical studies of plant–plant competition in two important ways: First, for simplicity, previous models have considered only intraspecific competition whereas many empirical ecologists are interested in both intra- and interspecific competition (Grime, 1979; Tilman, 1982; Wilson, 1988; Goldberg *et al.*, 1999; Semchenko *et al.*, 2007, 2010; Lamb and Cahill, 2008; Mommer *et al.*, 2010). To examine interspecific competition, it will be important to capture differences in uptake kinetics among species (Craine *et al.*, 2005; Craine, 2006), and here we build these uptake kinetics into a game-theoretic model of plastic root allocation. Second, several previous models (Gersani *et al.*, 2001; O'Brien *et al.*, 2007; O'Brien and Brown, 2008) examined an experimental design where soil resources per plant were held constant on a per-plant basis – that is, the models controlled for independent effects of neighbours and nutrients and isolated only neighbour effects. However, most empiricists grow plants in the same resource environment regardless of how many plants are present – that is, many experiments use a design where plants grown alone have access to at least twice as many resources than plants grown with neighbours. In this second type of experiment, plants grown alone are significantly larger than plants with neighbours (e.g. Cahill *et al.*, 2010), making it difficult to compare past modelling efforts with empirical studies.

Here, we present a game-theoretic model of root competition to (1) consider both intra- and interspecific competition by (2) explicitly considering the roles of uptake capacity, per-root costs, and nutrient levels for the degree of root production when plastic plants are grown alone and when grown with neighbours, and (3) explore game-theoretic predictions for root production strategies in the more common experimental design where soil resources are held constant regardless of how many plants are present. This approach allows us to extend game-theoretic predictions (Gersani *et al.*, 2001; O'Brien *et al.*, 2007; O'Brien and Brown, 2008) to the experimental systems that are most commonly used by plant ecologists, and generate some novel hypotheses for intra- versus interspecific competition, and how the traits of competitors shape root allocation responses. We conclude by suggesting three empirical tests which follow from the model that we believe can move forward the debate about whether plants engage in competitive games.

THE MODEL

We consider root allocation strategies by either one or two annual plants occupying an equal resource space regardless of how many plants are present. In all analyses we assume that soil nutrients are limiting, and that plants are not carbon limited. We extend previous game-theoretic models of plant root competition (Gersani *et al.*, 2001; O'Brien *et al.*, 2007; O'Brien and Brown, 2008) to address interspecific competition by introducing an element of uptake rate into the model and by holding resource levels constant regardless of the number of plants present. We employ a phytometer approach to model interspecific competition and imagine a series of variable focal plants competing against a constant neighbour (e.g. Cahill, 1999, 2002; Keddy *et al.*, 1994; Hedges *et al.*, 1999). The model is implicit with respect to space, and assumes infinite mixing of nutrients.

Let R represent soil resource levels at time zero (units of nutrient concentration). Let u_i be the root production strategy of plant i (units of biomass). Let c_i be the cost per-unit root of plant i (in units of resources per unit root). We model uptake capacity as a function of the encounter rate between nutrients and roots. Let a_i represent the effective encounter rate of a given unit of root biomass of plant i for the available nutrients (units of per time per unit root biomass). Throughout, parameters of the focal plant are denoted by subscript f, and parameters of the neighbour are denoted by subscript n. Following O'Brien *et al.* (2007), we use a saturating function to model total resource harvest, $H(r)$, as a function of resource levels and total roots in the community:

$$H(r) = R(1 - e^{-r}), \tag{1}$$

where $r = a_f u_f + a_n u_n$. The term r represents the total uptake capacity of the roots of the two plants combined. This formulation assumes a saturating relationship between root production and nutrient capture. Plants can increase their harvest by producing more roots, but root production gives diminishing returns and reaches a plateau. Equation (1) also provides a mechanism of nutrient depletion and ensures nutrients are depleted over the growing season when integrated over time. Time is scaled to be one growing period or season, thus the strategy (u_i) used by each plant represents the root production at senescence of an annual plant. Alternatively, perennial plants grow over many seasons, which means that their root mass (u_i) may change in each season, and that this model should only be applied to perennial plant competition with caution.

We let each plant's share of the nutrient harvest (H_i) be proportional to its contribution to the uptake capacity of roots in soil (we write this for the focal plant, but a similar expression with switched subscripts holds for the neighbour plant):

$$H_f = H(r) a_f u_f / (a_f u_f + a_n u_n). \tag{2}$$

Finally, let net profit or lifetime fitness be equal to the focal plant's share of the harvest (H_i)

minus the costs of producing the total root system (c_iu_i). Assuming total root system costs increase linearly with root production,

$$\pi_f = H_f - c_f u_f. \tag{3}$$

The best response curve

Before we proceed, we must introduce the concept of best response curves. In our model, we assume that plants assess and respond to their competitive environment. That is, plants are hypothesized to adjust their root allocation strategy relative to the root allocation strategy of their opponent and the resource environment. Thus, for each plant we can plot their best possible root allocation response as a function of the strategy played by the neighbour. For the present game of plant root competition, there are two best response curves – one for the focal plant and one for the neighbour (Fig. 1). These should be read as a sort of competitive play book for each plant: 'if the neighbour plant produces *y* roots, then the focal plant's best response is to produce *x* roots', and vice versa. However, since the two plants are hypothesized to have plastic responses, and to respond to the strategy of the other plant, this drives the system towards the point where the two curves cross. This point is the evolutionarily stable strategy (ESS). At the ESS point each plant can do no better, and this point is the only stable solution. Indeed, this ESS point is a true Nash equilibrium where each plant achieves maximum net profit (not shown, but can be calculated from equation 3) from nutrient harvest given the strategy of the other plant. If the plants produce fewer roots than the ESS, they receive a lower harvest and a lower profit, whereas if they produce more roots than the ESS, they pay a higher total root system cost, which also lowers profit. This will always drive the system towards this ESS point.

In the present game, there are three points along each curve of ecological interest, although we focus on only two of them. First, where the best response of the focal plant is zero, this shows the root mass that the neighbour would need to produce to exclude the focal plant (Fig. 1A). At this point, the neighbour produces such an extreme amount of roots that it captures almost all of the resources and the focal plant simply cannot achieve a positive growth rate. However, we do not expect this to be a common strategy and thus we do not consider this point in detail. Second, when the neighbour's root production is equal to zero, this is equivalent to the absence of a neighbour and this point on the curve shows the ESS root production of a plastic plant when it is grown alone (Fig 1A). Third, as described above, the point at which the focal and neighbour plants' curves cross represents equilibrium in root production of the two plants and is the ESS (Fig. 1B). At the ESS, neither plant has an incentive to change its strategy unilaterally, so the plants simultaneously balance resource harvest with neighbour pre-emption relative to resource levels and their species-specific per-root costs, and uptake efficiency.

Symmetric versus asymmetric games

We must also introduce the concept of symmetric versus asymmetric games. Previous modelling attempts have been symmetric games (Gersani *et al.*, 2001; O'Brien *et al.*, 2007; O'Brien and Brown, 2008), while the present model is an asymmetric game that allows us to investigate predictions for interspecific or intraspecific competition. When both plants have the same uptake and per-root cost parameters, then their best response curves are symmetrical, and the game is a *symmetric game* (Fig. 1B). Because the two plants employ the same strategy, in

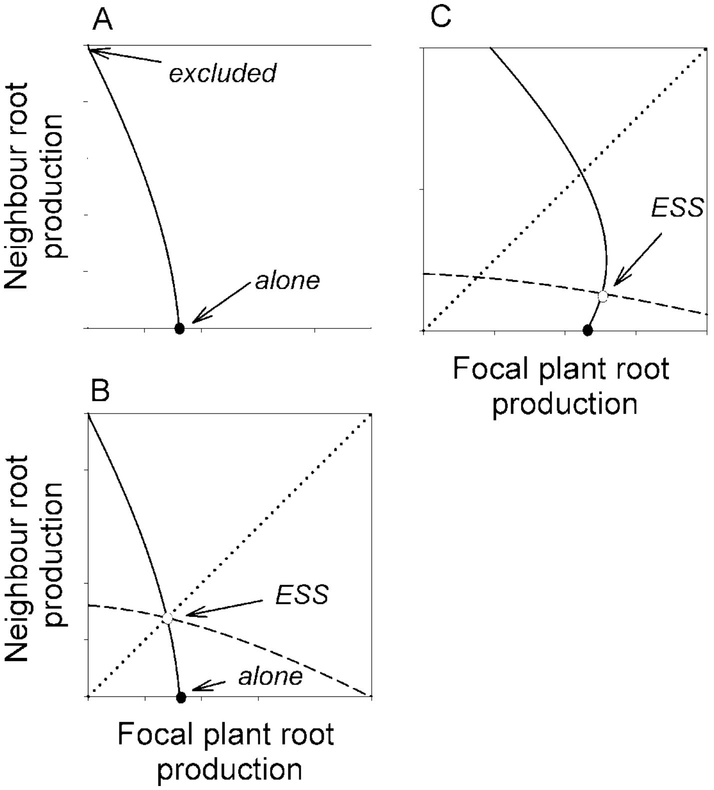

Fig. 1. Examples of best response curves for two competing plants. (A) Best response curve for a focal plant given the set of potential responses by a neighbour (not shown). When the neighbour response is equal to zero, this shows the best response of the focal plant when it is alone (solid circle). (B) Example of a symmetric game and intraspecific competition: here the neighbour's best response curve is added to the plot (dashed line), and because the plants are the same species, the neighbour's best response is identical to that of the focal plant. The ESS is the point where the two curves cross (open circle). A 1 : 1 reference line is also shown (dotted line), and in intraspecific competition (a symmetric game) the ESS will always fall on this line. (C) Example of an asymmetric game, and interspecific competition: here the neighbour (dashed line) is a different species and therefore has a different strategy set from the focal plant. As a result, the ESS will not fall on the 1 : 1 line.

a symmetric game the ESS always falls along the 1 : 1 line. Changing parameters (while keeping them identical for both plants) will expand or contract the curves and the ESS will simply move up or down the 1 : 1 line. A symmetric game most closely models intraspecific competition, where both competitors have relatively similar per-root costs ($c_f = c_n$) and uptake capacity ($a_f = a_n$). For interspecific competition, the competing plants will likely have different uptake ($a_f \neq a_n$) and per-root costs ($c_f \neq c_n$). Thus, two different species will likely play an *asymmetric game*, meaning their best response curves will have different shapes (Fig. 1C). In an asymmetric game, the ESS for each plant still occurs at the intersection of the best response curves; however, this point will not fall on the 1 : 1 line (Fig. 1C). Note that we use the words 'symmetric' and 'asymmetric' in the game-theoretic sense to refer to symmetry in strategies used (Fig. 1). This differs from the way that plant ecologists use the words ‘symmetric’ and ‘asymmetric’ to describe competitive effects based on plant body size, and should not be confused.

Single plant – root production in the absence of neighbours

Throughout we consider the optimal strategy of a focal plant by taking the derivative of condition (3) with respect to u_f and setting u_n equal to zero. To maximize fitness with respect to root production, the focal plant’s optimal root strategy must therefore satisfy condition (4):

$$d\pi_f/du_f = 0 = dH_f/du_f - c_f. \tag{4}$$

For plants grown alone, this can be solved analytically and yields an optimal root production (u_f*) of:

$$u_f{}^* = [\ln(a_f R/c_f)]/a_f. \tag{5}$$

Thus, for each plant we use these equations to calculate its expected root production when it is grown alone.

Two plants – root production in the presence of a neighbour

When there are two plants, the optimal root strategy of the focal plant (u_f) must satisfy condition (4), but it now depends on the root strategy of the neighbour (u_n). In this way, both plants deplete the resource and the root production of the neighbour influences the root production and harvest of the focal plant (and vice versa). The optimal root production of the focal plant, given the strategy of the neighbour, must therefore satisfy the following equation, and must be simultaneously optimized for both plants:

$$\frac{a_f R}{r}\left[\frac{a_n u_n}{r}(1 - e^{-r}) + a_f u_f e^{-r}\right] = c_f. \tag{6}$$

While this expression can only be solved numerically, it does show several features. First, the left-hand side represents the marginal benefit to the focal plant of producing more roots in the presence of its competitor based on the strategy of the competitor. This marginal benefit is influenced by the roots of the other plant, u_n, and by almost all of the parameters including the uptake ability of the neighbour (a_n). The only parameter that does not influence the focal plant root strategy directly is c_n, the per-root cost to the neighbour plant. Condition (6) can be used to numerically determine the optimal root strategy (u_f*) of the focal plant (a similar expression holds for the neighbour with reversed subscripts) in response to a range of root strategies (u_n) of the neighbour. This produces the *best response curves* for each plant when grown with neighbours (e.g. Fig. 1), and we can numerically determine the ESS root production.

Numerical simulations

We used numerical simulations to explore each plant’s best response curves and their ESS when grown with neighbours (equation 6), and to compare this with the ESS when plants are grown alone (equation 5). We present the results in three ways. First, we show a subset of the best response curves to show how altering one parameter at a time changes the larger set of potential best responses, and the ESS. Second, we focus on the two points of the best response curves that represent the ESS of plants either grown alone (equation 5) or with neighbours (equation 6), and plot each point as a function of the model parameters to demonstrate the more general relationship between the ESS strategy and each parameter of the model. Third, we investigate the degree to which plastic plants make trade-offs between efficiently harvesting nutrients and pre-empting neighbours in parameter space.

To do this, we take the ratio of ESS root production when neighbours are present versus when grown alone and plot these ratios as isolines, with the ratio as the z-axis and the model parameters as the x- and y-axes. This ratio will be less than 1 when plants make fewer roots with neighbours compared with when alone, indicating root production is focused on efficiently harvesting nutrients instead of pre-empting neighbours through high levels of over-proliferation. Alternatively, this ratio is greater than 1 when plants make more roots with neighbours compared with when alone, indicating a strong investment in neighbour pre-emption through over-proliferation of roots. We also discuss the role of root foraging efficiency, which we define as the ratio of uptake capacity and per-root cost (a_i/c_i). This ratio determines competitive ability of a plant in our model, and greatly influences the root strategy used by plants in interspecific competition. Low foraging efficiency indicates that plant roots possess some combination of low uptake ability and high per-root cost, which makes the plants weak competitors. Alternatively, high foraging efficiency involves some combination of high uptake ability and low per-root cost, and makes the plants strong competitors.

RESULTS

Intraspecific competition – a symmetric game

For intraspecific competition, increasing soil fertility (R) while holding per-root costs (c_i) constant increases the profit (π_i) to a foraging plant regardless of whether it is grown alone or with neighbours, and thus generally increases the ESS level of root production for all plants (equation 3). Indeed, changing resource levels is hypothesized to have a stronger effect on what a plant does with an intraspecific neighbour compared with when it is grown alone. This can be seen with the best response curves, where high values of R cause the best response curves of both plants to bow up and outwards away from the origin leading to a steep hump-shaped best response curve and high investment in neighbour pre-emption (Fig. 2A). Low resource levels are hypothesized to produce a more limited root production strategy where limited nutrient supply means that plants are more concerned with efficient nutrient harvest than pre-empting neighbours (Fig. 2A). This difference is driven by resource limitation. At low resource levels, plant growth is quite limited, giving the plants a much lower capacity to devote resources to over-proliferation of roots, and these severely resource-limited plants must focus more on simple efficient nutrient harvest. However, at high resource levels, resources become relatively less limiting, and the plants have more resources available to devote to over-proliferation of roots. More generally, along a gradient of increasing soil fertility, the ESS strategy with neighbours increases monotonically, while the ESS strategy when grown alone is a saturating function (Fig. 2B). Thus, as resource levels increase, the difference between ESS root production with neighbours compared with when grown alone becomes greater, with increasing levels of over-proliferation. This prediction is only valid when the assumption of no light limitation is met and under conditions where soil resources are still limiting to plant growth.

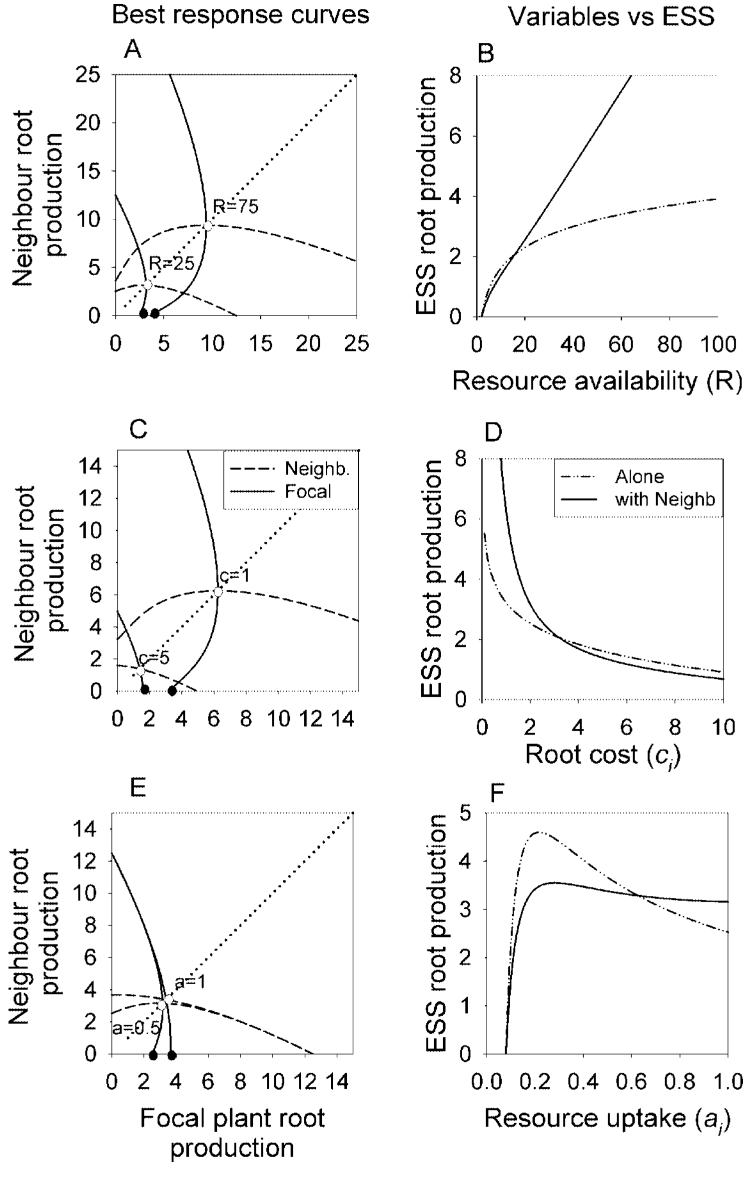

Fig. 2. Best response curves for two plants engaged in intraspecific competition (i.e. a symmetric game) (A, C, E). In all panels, the ESS alone (solid circle) and the ESS with neighbours (open circle) are highlighted. The relationship between each variable and the ESS with and without neighbours for a symmetric game is also shown (B, D, F). (A) Best response curves for two plants as resource availability shifts ($R = 25$ and $R = 75$ shown; $a_f = a_n = 1.0$, $c_f = c_n = 2$). (B) Relationship between resource level and the ESS when plants are alone (dashed line) or with neighbours (solid line). (C) Best response curves for two plants as root cost varies ($c_f = c_n = 5$ and $c_f = c_n = 1$ shown; $a_f = a_n = 1.0$, $R = 25$). (D) Relationship between root cost and the ESS when plants are alone (dashed line) or with neighbours (solid line). (E) Best response curves for two plants as uptake capacity varies ($a_f = a_n = 0.5$ and $a_f = a_n = 1.0$ shown: $c_f = c_n = 2$, $R = 25$). (F) Relationship between uptake capacity and the ESS when plants are alone (dashed line) or with neighbours (solid line).

Differences in the base cost per-root (c_i) are similar to changing resource levels, in that lower per-root costs lead to higher net profits (π_i) for each plant regardless of whether it is grown alone or with an intraspecific neighbour (equation 3). As with resources, differences in per-root cost are hypothesized to have a greater impact on what the plant does with neighbours than what it does alone. For best response curves, decreasing root costs bows the curves up and away from the origin (Fig. 2C) in a manner that is roughly similar to increasing resource availability (Fig. 2A). However, more generally the relationship between cost and ESS root production is a negative exponential curve for both plants grown alone and with neighbours (Fig. 2D). This means that small differences in per-root costs among competing plants are hypothesized to have dramatic effects on ESS root production, making per-root metabolic costs a key variable for determining the outcomes of root competition. This occurs because plants with higher per-root costs obtain lower marginal benefits from root production, and the plants are hypothesized to focus more on efficient resource harvest than neighbour pre-emption and often produce fewer roots with neighbours than when grown alone (Fig. 2D). In contrast, plants with lower per-root costs are hypothesized to obtain higher marginal benefits and thus focus more on resource pre-emption, and are predicted to strongly over-proliferate roots in response to competition (Fig. 2D).

Different from R and c_i, changing root uptake rates (a_i) in a symmetric game is hypothesized to impact what the plant does when grown alone more than when it has neighbours (Fig. 2E). The shape of the best response curves (Fig. 2E) changes little with a_i except at the lowest values of a_i where plants cannot effectively capture nutrients, and perform poorly. This produces an asymmetrically hump-shaped relationship between uptake ability and ESS root production (Fig. 2F). At low values of a_i roots are ineffective, and so there is little profit for increasing root production, and thus the plants focus more on efficient nutrient harvest than on neighbour pre-emption. However, plants with higher uptake capacity can profit from increased root production but this quickly reaches a maximum, beyond which root production declines slightly with increasing uptake ability (Fig. 2F). This maximum root production occurs when $a_f = c_f e^{-(R/c)}/R$ for plants grown alone, but must be found numerically for plants grown with neighbours.

To investigate this difference between efficiently harvesting nutrients and pre-empting neighbours over a wider range of parameter space, we take the ratio of ESS root production when with neighbours versus when grown alone and plot these ratios as contour plots within the parameter spaces of R and a (Fig. 3A), c and a (Fig. 3B), and R and c (Fig. 3C). When the ratio is greater than 1, the plants produce more roots in the presence of neighbours than when grown alone, and we conclude the ESS is to focus heavily on neighbour pre-emption through over-proliferation of roots. When the ratio is less than 1, plants produce fewer roots in the presence of neighbours than when grown alone, and we conclude the plants focus on efficient resource harvest rather than neighbour pre-emption. The numerical results show that plant responses may be quite variable. Of particular interest is that by using an experimental design where pot volume is held constant, there are many regions of parameter space where plants produce fewer roots in the presence of neighbours than they do when grown alone. Specifically, plants experiencing intraspecific competition are hypothesized to make fewer roots in the presence of neighbours compared with alone when they are most limited by resource availability, root costs are high or uptake ability is low (Fig. 3), even while they engage in a game-theoretic strategy.

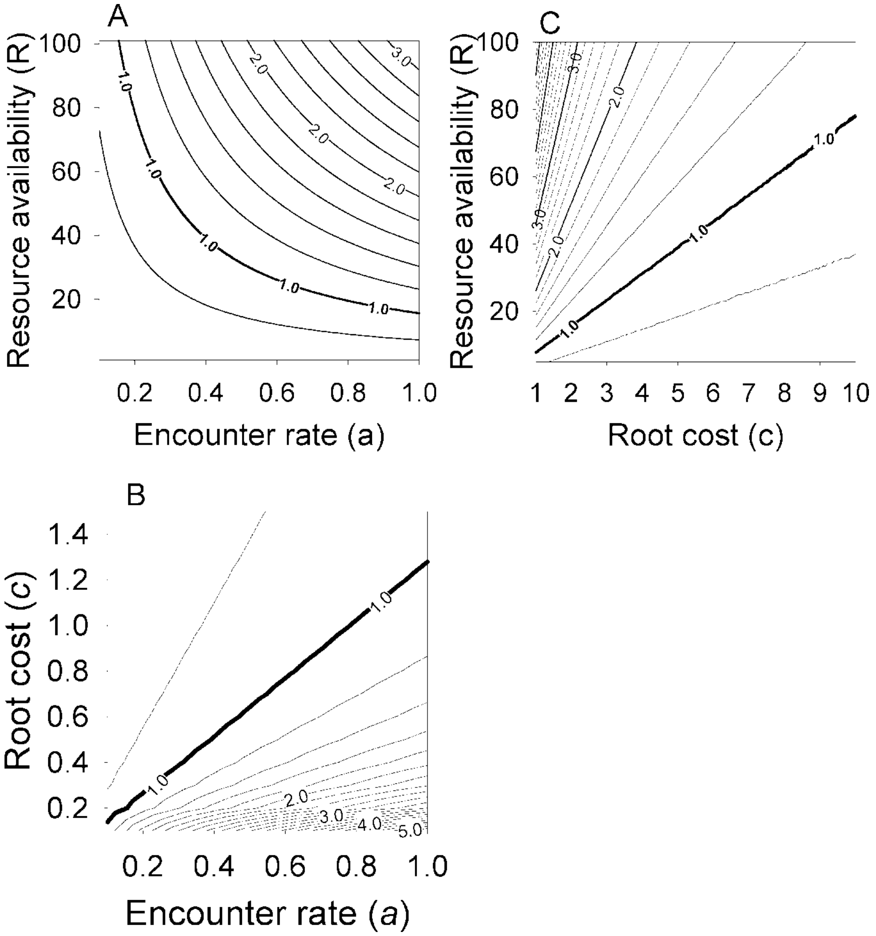

Fig. 3. Isolines for the ratio of ESS root production when neighbours are present divided by ESS root production when alone. Ratios less than 1.0 occur when plants make fewer roots with neighbours than when alone, and ratios greater than 1.0 occur when plants make more roots with neighbours than when alone. The 1.0 isoline that borders these two regions is highlighted in all panels. (A) Resource availability and uptake capacity are varied, $c_f = c_n = 2$. (B) Root cost and uptake capacity are varied, $R = 25$. (C) Resource availability and root cost are varied, $a_f = a_n = 1$.

Interspecific competition – an asymmetric game

We modelled interspecific competition as an asymmetric game by assuming the competing plants have different uptake abilities and/or different root costs: $a_f \neq a_n$ and $c_f \neq c_n$ (e.g. Fig. 1C). As a result, unlike above, each plant may have a different root strategy at the ESS (the best response curves no longer intersect along the 1:1 line) (Fig. 1C). Following a phytometer approach, we vary parameter values for the focal plant, while fixing those for the neighbour at intermediate values of uptake rate and root cost ($c_n = 5$, $a_n = 0.7$; $a_i = 0.7$ is not numerically intermediate, but it was biologically intermediate because of the relationship between a_i and root production; Fig. 2F). The range of parameters allowed us to explore how root production shifted when the focal plant had both lower and higher root efficiency than the neighbour.

For interspecific competition, the univariate relationships between ESS root production and resource levels, root costs or uptake rate are similar to intraspecific competition (Fig. 4). As resources (R) increase or costs (c_i) decrease, the ESS root production for the focal plant will similarly increase, causing the best response curves to bow up and outwards (Fig. 4). A change in uptake (a_i) continues to have a relatively small effect on ESS root production (Fig. 4F). However, there are some key differences between the predictions for intra- and interspecific competition.

In this analysis of interspecific competition, the two plants have different traits and thus may differ in what we define as root foraging efficiencies (a_i/c_i). Root foraging efficiency now begins to become important for generating hypotheses about root allocation, and the strategies used when plants face an interspecific neighbour. The model predicts that a high-efficiency plant competing with a low-efficiency plant should exhibit a high over-proliferation response (Fig. 4). High-efficiency plants are hypothesized to invest heavily in pre-empting their neighbours because they have some combination of increased ability to capture resources and decreased costs of producing roots that gives them a competitive advantage over a less efficient neighbour. In contrast, low-efficiency plants are hypothesized to have a relatively muted response and rarely change strategy in the presence of a high-efficiency neighbour (Fig. 4). These plants have best response curves that are often almost flat, indicating they are expected to exhibit only a small response to the presence of a range of potential neighbours. This occurs because their roots are costly, and they have a lower ability to capture resources. In short, they are weaker competitors and thus their best response is to curtail root production and focus on harvesting resources as efficiently as possible in the face of a fight they cannot win. These two different causes make both plants produce fewer roots in interspecific competition compared with intraspecific competition.

As above, we plotted the focal plant's ratio of root production with neighbours versus alone as contour plots in the parameter spaces of R and a_f (Fig. 5A), c_f and a_f (Fig. 5B), and R and c_f (Fig. 5C) to explore trade-offs in investment in efficient nutrient harvest versus neighbour pre-emption. For interspecific competition (relative to intraspecific competition), there was an increased amount of parameter space where the plants produced more roots alone then when grown with neighbours, indicating a trend towards reduced investment in neighbour pre-emption and generally more investment in efficient resource harvest. Interestingly, the interaction between resource availability and resource encounter rate changed for interspecific competition (Fig. 5A) versus intraspecific competition (Fig. 3A). Here differences in root foraging efficiency drove this effect as described in the preceding paragraph.

DISCUSSION

Above, we detail some predictions of a game-theoretic model of intraspecific (Figs. 2, 3) and interspecific (Figs. 4, 5) plant root competition, with the primary goal of understanding the conditions that lead to differential investment in efficient resource capture (low root proliferation) versus pre-empting neighbour resource supplies (over-proliferation). Following the more common experimental design, we modelled a situation where plants were grown in a constant resource space regardless of how many plants were present. Competing plants could vary in per-root costs or in nutrient uptake ability and the

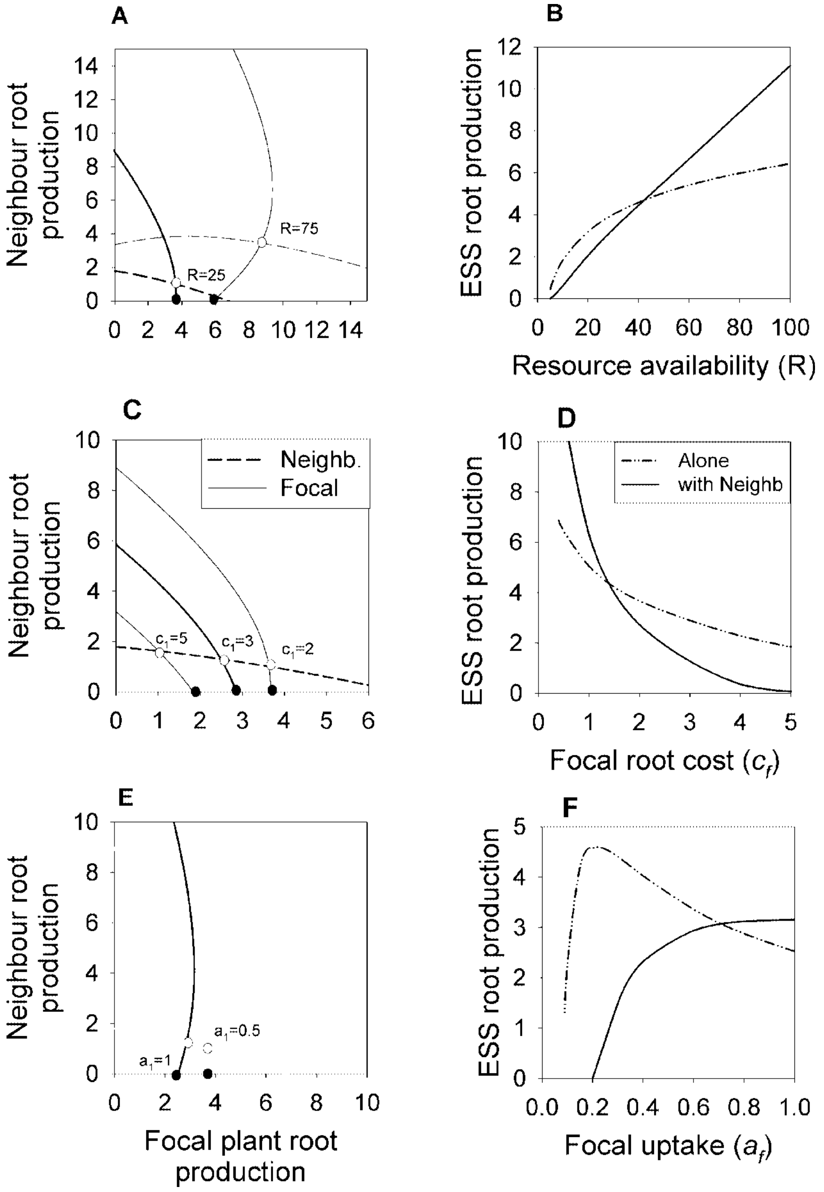

Fig. 4. Best response curves for an asymmetric game. In all panels, the ESS alone (solid circle) and the ESS with neighbours (open circle) are highlighted. (A) Best response curves as resource availability shifts ($R = 25$ and $R = 75$ shown; $c_f = 2$, $c_n = 5$, $a_f = 0.5$, $a_n = 0.7$). (B) Relationship between resource level and the focal plant's ESS when grown alone (dashed line) or with neighbours (solid line). (C) Best response curves as the root cost of plant 1 only varies ($c_f = 5$, $c_f = 3$, and $c_f = 2$ shown; $a_f = 0.5$, $c_n = 5$, $a_n = 0.7$, $R = 25$). (D) Relationship between root cost and the focal plant's ESS when grown alone (dashed line) or with neighbours (solid line). (E) Best response curves for two plants as the uptake capacity of plant 1 only varies ($a_f = 0.5$ and $a_f = 1.0$ shown; $c_f = 2$, $c_n = 5$, $a_n = 0.7$, $R = 25$). (F) Relationship between uptake capacity and the focal plant's ESS when grown alone (dashed line) or with neighbours (solid line).

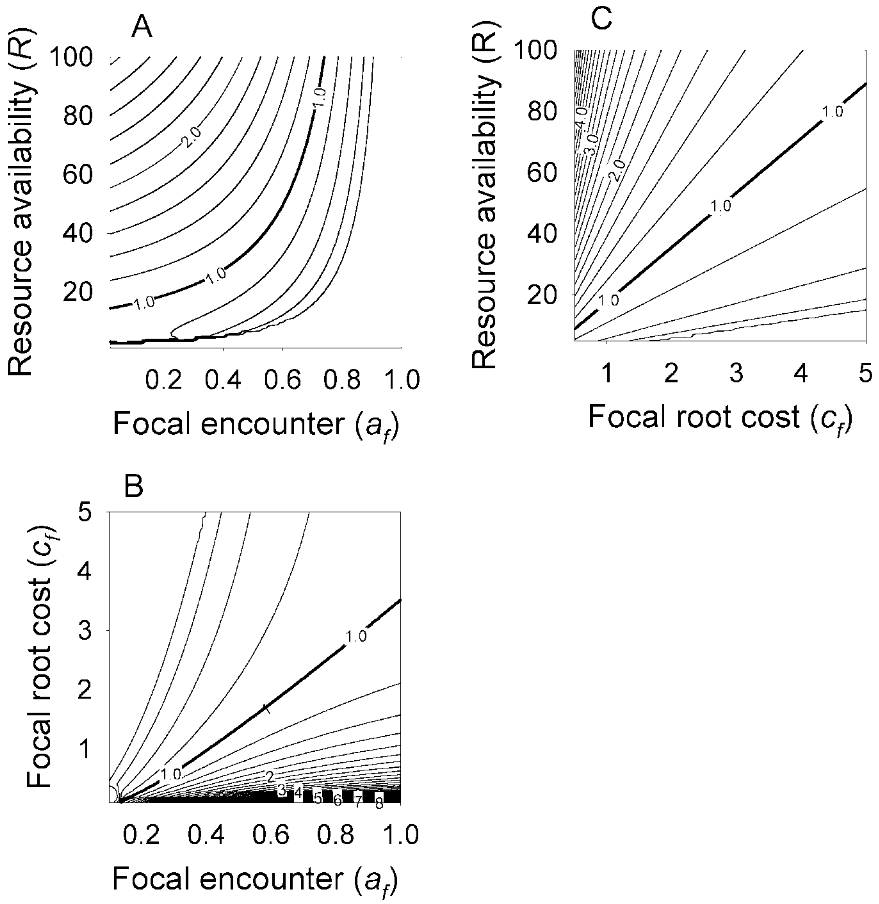

Fig. 5. Isolines for interactions among parameter values for the focal plant in an asymmetric game. The z-axis is the ratio of ESS root production when neighbours are present divided by ESS root production when alone. Parameters for the neighbour were held constant in all simulations: $a_n = 0.7$, $c_n = 5$. (A) Resource availability (R) and uptake capacity of the focal plant (a_f) was varied, and $c_f = 2$. (B) Root cost (c_f) and uptake capacity (a_f) for the focal plant only were varied, and $R = 25$. (C) Resource availability (R) and root cost for the focal plant (c_f) only were varied, and $a_f = 0.5$.

environment could vary in soil fertility. Similar to previous game-theoretic models of root competition (Gersani *et al.*, 2001; Craine *et al.*, 2005; Craine, 2006; O'Brien *et al.*, 2007; O'Brien and Brown, 2008; Dybzinski *et al.*, 2011), the model predicts that plants often invest heavily in pre-empting their neighbours by over-proliferating roots in many regions of parameter space (Figs. 3, 5). However, due to the experimental design adopted, the present model also predicts that there are wide regions of parameter space where plants are expected to invest more heavily in efficient resource capture and exhibit a much lower degree of root proliferation when neighbours are present compared with when they are grown alone (Figs. 3, 5). However, we emphasize that this reduced root growth in the presence of neighbours relative to being grown alone was due to our use of a constant resource space regardless of whether plants were grown alone or with neighbours and was expected for plants that experience intraspecific (Figs. 2, 3) or interspecific competition (Figs. 4, 5). This modelling approach is more consistent with experimental approaches (Schenk, 2006; Hess and de Kroon, 2007), but it gives plants grown alone at least twice as many resources as they receive when grown with neighbours.

A primary goal was to examine predictions for root production strategies when plants experience interspecific competition. In general, the model predicts that plants that experience interspecific competition generally are predicted to exhibit less over-proliferation of roots relative to plants that experience intraspecific competition. This effect was driven by the relative foraging efficiency of the neighbour compared with the focal plant. When facing an interspecific neighbour that was more efficient, a plastic focal plant is hypothesized to focus its root production primarily on efficient nutrient harvest, and the resulting over-proliferation is limited. This happens because the less efficient plant is at a competitive disadvantage, and its ability to over-proliferate roots is limited by its reduced capacity to capture and invest resources in further root growth. In contrast, the more efficient plant is at a competitive advantage and is expected to behave almost as if the inferior neighbour is absent. These more efficient plants have essentially already won the competition due to their superior nutrient uptake ability, and therefore do not waste resources over-proliferating roots against an inferior neighbour.

We modelled plant root production based on the relatively controversial assumption that plants can assess and respond to their resource environment and to the presence of neighbours through plasticity in root production. Despite disagreement in the literature (Laird and Aarssen, 2005; Schenk, 2006; Hess and de Kroon, 2007; Semchenko *et al.*, 2007, 2010; de Kroon *et al.*, 2012), current data support the idea that at least some plants can assess and respond to the presence of neighbour cues (Schenk *et al.*, 1999; Dudley and File, 2007; Cahill *et al.*, 2010; Mommer *et al.*, 2010; Semchenko *et al.*, 2010), although the exact nature of these cues remains largely unknown (Falik *et al.*, 2003, 2005, 2011; Novoplansky, 2009; see discussion below). However, results have been mixed and they show that plants may sometimes produce more (Gersani *et al.*, 2001; O'Brien *et al.*, 2005; Semchenko *et al.*, 2007; Mommer *et al.*, 2010) or less (Litav and Harper, 1967; Schenk *et al.*, 1999; Semchenko *et al.*, 2007, 2010; Cahill *et al.*, 2010) roots in the presence of neighbours compared with when grown alone. This range of results has been used to challenge the predictions of game-theoretic models of root competition (Schenk, 2006; Hess and de Kroon, 2007; Semchenko *et al.*, 2007), leading some to go as far as to reject the importance of competition altogether (de Kroon *et al.*, 2012). However, many empirical results are not directly comparable with the predictions of previous game-theoretic models because of the way space and resources per plant are controlled in the model compared with experimentally. Specifically, past models held resources per plant constant (e.g. Gersani *et al.*, 2001; O'Brien *et al.*, 2007; O'Brien and Brown, 2008), while most empiricists offer plants grown alone twice as many resources as plants grown with neighbours (e.g. Schenk, 2006; Hess and de Kroon, 2007; Cahill *et al.*, 2010; Mommer *et al.*, 2010). In the present study, we modelled this second experimental approach, which allows us to make predictions about the type of system that is more commonly studied by empiricists. By modelling the type of experiment that is more commonly performed, the present model provides some context with which to understand the range of empirical results that have been observed. For example, in such an experimental design, and for interspecific competition, over-proliferation is predicted to be most important in systems with lower nutrient limitation (e.g. high productivity), for plants with low root costs, and for plants with high uptake ability (Fig. 5). In contrast, in highly nutrient-limited systems, neighbour pre-emption is probably less important.

A key prediction of this model is that root over-proliferation increases with increasing soil nutrient availability (while nutrients are limiting to growth) when neighbours are present, but plateaus in the absence of competition (Figs. 2B, 4B). Roots have been traditionally difficult to study but data are rapidly accumulating on plant responses to neighbours below ground (Schenk, 2006) and there is research to support this prediction. Maina *et al.* (2002) grew *Phaseolus varigaris* where plants either had exclusive access to pots (owners) or had their roots split between two pots shared with neighbours (fence sitters) and the experiment was performed at two nutrient levels – high and low. The plants in this study always made more roots in the presence of neighbours than when grown alone, but the magnitude of over-proliferation was higher in the high nutrient pots versus the low nutrient pots. Similarly, Cahill *et al.* (2010) grew *Abutilon theophrasti* in either nutrient-poor homogeneous soil or in heterogeneous soil with a high-quality patch between the two plants. Using a mini-rhizotron camera and root staining, they were able to measure the root overlap of each plant as they competed in soil. Plants in the nutrient-poor homogeneous soil avoided neighbours leading to segregation in soil and low over-proliferation. However, when a nutrient-rich patch was placed between the two plants, the plants greatly expanded their root system leading to significant overlap of root systems inside the nutrient-rich patch (Cahill *et al.*, 2010). At the neighbourhood scale, Mommer *et al.* (2010) grew monocultures and mixtures of four co-occurring grassland species with a rich layer of nutrients either in the shallowest soil layers or in the deepest soil layers. They found significantly more root production in mixtures than expected if plants did not respond to neighbours. However, in the first year of the study, they observed strong over-proliferation only when nutrients were in the top layer (where most roots were), although by the second year, as roots moved into the deepest layers, both the shallow and deep nutrient treatments had significantly more roots than had been expected if plants did not respond to neighbours (Mommer *et al.*, 2010). Finally, at the global level, there are strong indications that fine root biomass is positively correlated with both nitrogen and phosphorus availability (Yuan and Chen, 2012). Taken together, these data suggest that increased root production with increasing nutrient availability is empirically possible, and even common at the global scale (Yuan and Chen, 2012). Our model suggests that the reason for this increased root production is not to capture more nutrients, but because the plants try to pre-empt the nutrient supply of their neighbours.

Of course, plants do not always over-proliferate roots (Novoplansky, 2009; Cahill and McNickle, 2011) (Figs. 2–5). There are many examples of root segregation (Parrish and Bazzaz, 1976; Mahall and Callaway, 1991; Schenk *et al.*, 1999) and reduced root production (Litav and Harper, 1967; Semchenko *et al.*, 2007; Cahill *et al.*, 2010) in the presence of neighbours. The model presented here provides testable predictions about when plants should limit their over-proliferation response in the presence of neighbours. Specifically, reduced over-proliferation is adaptive when resource levels are low, or when facing an interspecific neighbour with significantly higher or lower root foraging efficiency (Fig. 5). The model also assumes that nutrients are always limiting to growth. However, when nutrients are less limiting than carbon, plants may also minimize their root production in favour of shoot production. We suggest that research into below-ground competitive strategies move beyond the question of whether over-proliferation is possible, towards understanding the specific cues that lead to over- or under-proliferation of roots.

There are a number of caveats. First, our use of a type II functional response (equation 1) simplified many of the analyses and numerical analyses, but this assumption is not necessary. So long as a plant experiences diminishing returns to increasing root production, the use of a more sophisticated functional response (e.g. Michaelis-Menten kinetics) will not change the general shape of the best response curves or the qualitative predictions of our model. However, changing the underlying functional response of plants to resources would alter the quantitative predictions of our model. Second, we assumed per-root costs were constant regardless of total root production, but it is conceivable that per-root costs may either increase or decrease with increasing total root production. Changes in the way costs scale would change the predictions of the model. For example, if per-root costs decline with total root production, then root proliferation would become cheaper as the plants grow. Thus, it would be possible that the plant with the lowest root costs would over-proliferate so much that it might force the other to produce essentially no roots (e.g. Fig. 1A). This seems unlikely, but is not inconceivable. Conversely, if per-root costs increase with increasing root production, the qualitative results of such a model would be similar to those presented here. However, the quantitative predictions would change. Increasing per-root costs with increasing root production would cause the over-proliferation response to decline and would lead to increased investment in efficient nutrient harvest at the expense of neighbour pre-emption. Third, our model assumes no light limitation, and that nutrients are always limiting. However, light limitation or shoot competition would limit the carbon available to produce roots and thus would probably further minimize the over-proliferation response again, favouring efficient nutrient harvest over neighbour pre-emption. Fourth, our model predicts only the strategies of annual plants, and should be applied to perennial plants with caution. We fixed our time scale to one growing season, and for an annual plant this allows us to link root strategies to lifetime fitness. However, perennial plants play iterative games over many growing seasons, which should allow them to use more complex strategies and possibly alter their root strategy at each time step (e.g. Fransen and de Kroon, 2001; Mommer *et al.*, 2010) in ways our model is unable to predict. Fifth, the model is implicit with respect to space because we were primarily interested in total root production, and less interested in root placement. However, root placement is important, and plants must find resources in soils that are often heterogeneously distributed and this can influence competition (Cahill *et al.*, 2010; Cahill and McNickle, 2011). This could be remedied by including a spatial component, and by making nutrient transport a function of distance away from the stem. O'Brien *et al.* (2007) presented a similar game-theoretic model of root production in the presence of neighbours. In their model, they predicted similar root responses to those we have described above, except that the plants would only exhibit neighbour responses in regions of overlap with a neighbour's root system (O'Brien *et al.*, 2007).

A final caveat is that the mechanisms used by plants to detect and respond to neighbours are not well understood (Falik *et al.*, 2003; Schenk, 2006; Semchenko *et al.*, 2007; Novoplansky, 2009). It is known that at least some plants are capable of over-proliferation of roots because we can observe the root growth response of a plant grown alone and compare it with that of a plant grown with neighbours (e.g. Aphalo and Ballare, 1995; Maina *et al.*, 2002; Semchenko *et al.*, 2007, 2010). In this study, we were more interested in generating hypotheses about the ecological and evolutionary implications of these root responses, which can be modelled independent of any specific mechanism. However, it is worth discussing the hypothesized neighbour-sensing mechanisms in relation to our modelling choices. There are at least three different hypotheses that have been proposed in the literature as a potential mechanism for self/non-self discrimination in plants, none of which are well supported (or are refuted) by data at this time and thus we have incorporated the simplest mechanism into our model. First, it has been speculated that plants might produce a sort of electromagnetic signal that allows them to determine which roots are self and which are non-self (Novoplansky, 2009). This is an interesting idea, although to our knowledge there is no known mechanism or data to support the idea that plants either produce or sense such signals and we do not consider this further. Second, plants produce many chemical exudates in soils, and a more common hypothesis is that plants might use these root exudates as a cue to sense neighbours (Mahall and Callaway, 1991; Aphalo and Ballare, 1995; Schenk *et al.*, 1999). There is some limited support for this mechanism (Falik *et al.*, 2005; Semchenko *et al.*, 2007), although experimental methods have been plagued by difficulties in independently manipulating exudates and neighbours without confounding some other variable such as nutrient availability (Lau *et al.*, 2008). Furthermore, there is evidence that genetically identical clones are able to distinguish whether roots in soil are physiologically integrated with the focal plant, or part of some other disconnected clone (Falik *et al.*, 2003). This suggests that at a minimum exudates are not the whole story since genetically identical clones should have identical exudates. Another difficulty with this idea is that if plants have different responses to different neighbours as has been observed (e.g. Mommer *et al.*, 2010; Semchenko *et al.*, 2010), they would need a vast array of different sensory structures – one for every possible species they might encounter – to allow them to have a species-specific neighbour response. Modelling such a mechanism would be unnecessarily complex given that there is limited support for this hypothesis. The third and simplest mechanism – the one we have modelled – is that plants use changes in nutrient levels to detect neighbours indirectly through neighbour effects on nutrient levels (Aphalo and Ballare, 1995; Gersani *et al.*, 2001; O'Brien *et al.*, 2007; O'Brien and Brown, 2008). Unlike the first two mechanisms, it is well known that plants are capable of sensing nutrient levels, and that plants adjust both root branching and root growth as a function of resource levels (Zhang *et al.*, 1999; Zhang and Forde, 2000; Forde and Walch-Liu, 2009). The existence of well-understood genes associated with this idea, and the simplicity of this mechanism make it logically appealing. However, we caution that there currently is limited evidence to support these nutrient-sensing pathways as a mechanism for sensing neighbours. However, the diversity of knockout mutants of *Arabidopsis thaliana* available for many of these nutrient-sensing mechanisms (Zhang *et al.*, 1999; Zhang and Forde, 1998, 2000; Forde and Walch-Liu, 2009) would provide a powerful experimental system for testing this proposed mechanism. We have modelled this mechanism because it is the simplest mathematically and the simplest physiologically, and with a lack of evidence supporting alternatives, we argue that simplicity is prudent at this time. Furthermore, since we do not ask any questions about mechanism, it is still possible to develop hypotheses and discuss the ecological and evolutionary consequences of root over-proliferation independent of the consequences of any specific proximate mechanism.

Moving forward with tests of game theory

Models can only generate hypotheses about the world, not conclusions. Thus, the present model was designed to model the types of experiments that plant ecologists more commonly perform, and to make predictions about how plants might make trade-offs in root production based on uptake capacity and per-root costs when faced with intra- or interspecific neighbours. The current model predicts that, when pot volume is held constant, plants may often produce fewer roots in the presence of neighbours than when grown alone (Figs. 2–5), even while engaging in a tragedy of the commons game (*sensu* Gersani *et al.*, 2001). This is a result that more closely matches empirical results than previous explorations of plant competition as a game. We suggest that research in this area move past the question of whether it is possible for plants to respond to the presence of neighbours. That question has been unequivocally answered: plants can and do respond to the presence of neighbours by adjusting their root production, and this can involve either an increase or a decrease in root production (Semchenko *et al.*, 2007, 2010; Novoplansky, 2009; Cahill *et al.*, 2010; Mommer *et al.*, 2010). Instead, we suggest that plant ecologists ask *what environmental conditions and traits of the plants lead to either increased or decreased root production when neighbours are present compared with plants grown alone?* Understanding the contexts that can shift root allocation responses will lead to a better understanding of the importance of below-ground competition, and plant strategies for interacting with neighbours.

Based on the predictions of the present model, we suggest three new directions for the study of plant strategies for competition that can continue to drive the development of theory:

1. *How does allocation to root production change along a gradient of soil fertility both when plants are grown alone and with neighbours?* A basic assumption of the model is that root production is fundamentally different when plants are grown alone or with neighbours. Plants are hypothesized to increase root production monotonically along a gradient of soil fertility (while soil resources are still limiting to growth); plants experiencing root competition should increase at a faster rate than plants that do not experience competition (Fig. 2b). Alternatively, if plants do not respond to neighbours, as some argue (Hess and de Kroon, 2007; de Kroon *et al.*, 2012), then there should never be more roots in the presence of neighbours than when grown alone along this gradient. Data from the literature support our model (Maina *et al.*, 2002; Cahill *et al.*, 2010; Mommer *et al.*, 2010; Yuan and Chen, 2012), although these experiments were not designed to test this hypothesis.
2. *How does variable root foraging efficiency influence root production strategy in interspecific competition?* Another prediction of the model is that in interspecific competition, root foraging efficiency (defined as *per-root cost/encounter rate*) decisively predicts a plant's competitive ability, and root production strategy. If plants can assess and respond to cues from neighbours, the model predicts that plants should intensely over-proliferate roots against weaker competitors – gaining a large fitness and competitive advantage – but produce far fewer roots in the presence of stronger competitors – avoiding being burdened by high root costs when they are in a fight they cannot win. A test of this prediction could be achieved using a variety of plant species with different per-root metabolic costs and uptake capacities, and a phytometer approach. With enough taxonomic replication, such an experiment could begin to map empirical results onto the isolines presented in Fig. 5B. Care should be taken to obtain enough variation in root costs and uptake capacity to fully explore the parameter space. Similarly, care should be taken to compare relative foraging efficiency, not absolute foraging efficiency.
3. *How does shoot competition influence investment in neighbour pre-emption or efficient nutrient harvest*. The model assumes no shoot competition, plants are not light limited and are always nutrient limited. Thus, our model makes no quantitative predictions about how shoot interactions influence root strategies, or how plants might behave if they are more limited by carbon than by soil nutrients. However, qualitatively, we can say that shoot competition will decrease marginal benefits at the whole plant level and therefore cause a further reduction in investment in neighbour pre-emption than predicted by the present model. Empirical results that compare root strategies with and without shoot competition (e.g. Cahill, 2002) would be invaluable for developing predictive theory, and further understanding the range of strategies plants may use in soil.

Other experiments testing any of the patterns predicted in Figs. 2-6 are certainly possible, although we suggest that these three questions will lead to the most important insights into the nature of plant strategies, the types of cues to which plants respond, and the potential consequences of different plant strategies for plant-plant interactions.

CONCLUSIONS

We have presented a game-theoretic model that more closely matches the types of experiments ecologists commonly perform, and that accounts for differences in uptake ability that might occur among plants. We have also introduced the concepts of best response curves, symmetric versus asymmetric games, and root foraging efficiency. The model provides some context to understand the range of empirical results that have been observed, and we believe can clarify some of the current debate around whether and how plants respond to neighbours. A key finding is that plants that engage in competitive games vary considerably in the investment they make into pre-empting their neighbours through over-proliferation of roots. Specifically, over-proliferation is predicted to increase with increasing nutrient availability, and interspecific competition should generally result in less over-proliferation compared with intraspecific competition. We suggest that experiments need to move beyond the idea of whether plants respond to neighbours, and move towards an understanding of how environmental conditions and traits used by neighbours influence the responses of plants. Models can inform empirical inquiry, but only data can generate conclusions about the way that plants respond to neighbours. We have suggested three empirical tests that flow directly from the predictions of our model, which can be used to understand the nature of plant strategies but also to guide the development of future theory.

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