REGULAR ARTICLE

Optimal root proliferation strategies: the roles of nutrient heterogeneity, competition and mycorrhizal networks

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Abstract

Background and Aims Plants proliferate roots in order to acquire nutrients, typically contending with heterogeneous resources and competing neighbours. A mathematical model was developed to identify optimal root proliferation strategies in patchy nutrient environments. The impact of joining mycorrhizal networks was also assessed.
Methods A simple model of growth and competition in one spatial dimension was implemented within a genetic algorithm to obtain optimal proliferation strategies under different scenarios of resource distribution, and in the presence or absence of local competition and large-scale mycorrhizal networks.
Results A strong proliferation response emerged for isolated plants in heterogeneous environments with low resources, and also for plants growing in competition. Even in statistically homogeneous environments, the presence of competition conferred a selective advantage to plants proliferating in the direction of the most recently acquired patch. In the presence of mycorrhizal networks, the optimal strategy switched from symbiosis to proliferation driven growth as the relative cost of acquiring resources through the networks increased.
Conclusions The optimal proliferation response in a given scenario was governed by a hierarchy of factors: resource levels and distribution; the presence or absence of competition; and the marginal benefit of obtaining resources via symbiotic relationships with mycorrhizas.

Keywords Plant roots · Nutrient patches · Foraging · Arbuscular mycorrhizas · Mathematical modelling

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Introduction

Nutrient availability in soil is both spatially and temporally heterogeneous over relatively small distances and at scales relevant to plant roots (Cain

et al. 1999; Jackson and Caldwell 1993; Farley and Fitter 1999; Gross et al. 1995). Plant roots have to cope with this heterogeneity or patchiness in resource supply and be able to exploit the nutrient-rich zones or patches upon encounter. Moreover, they have to capture nutrients from such patches both in competition with soil organisms and other plant root systems (Hodge et al. 2000a, b; Kaye and Hart 1997). Plants are aided in this respect by the modular structure of their roots systems, which enables architectural flexibility in root deployment (de Kroon et al. 2009; Malamy 2005; Hodge et al. 2009). Localized root proliferation in nutrient-rich patches is a well established response to heterogeneity in resource supply (reviewed by Hodge 2004, 2009) although it has also been demonstrated that root proliferation is of little net benefit to either single plants or plants grown in monoculture as a means to acquire nitrogen (N) from N-rich zones (Hodge et al. 1998a; Fransen et al. 1998; van Vuuren et al. 1996). This is due to the high mobility of nitrate (NO_3^-) ions, which in moist soil have a diffusion coefficient in the region of $10^{-5} cm^2 s^{-1}$ (Tinker and Nye 2000). However, when plants are grown in interspecific competition for N from a complex organic patch (mixed N-sources) then root proliferation does confer a competitive advantage (Hodge et al. 1999a; Robinson et al. 1999). In contrast to NO_3^- ions, phosphate ions are relatively immobile with a diffusion coefficient in moist soil of around $10^{-9} cm^2 s^{-1}$ (Tinker and Nye 2000). Given the rate of growth and the average lifespan of the finer roots (see Fitter 1999; Eissenstat and Yanai 1997) which are responsible for much of the nutrient uptake, the relative volumes of soil able to be exploited for these different nutrients by a single root per unit root length can differ by orders of magnitude (Fitter et al. 2002). Consequently, whilst a plant's root system can capture NO_3^- from a relatively large surrounding area, successfully obtaining phosphate from the environment requires a plant either to proliferate roots directly within the phosphate sources, or to use another strategy e.g. forming a symbiotic relationship with mycorrhizal fungi.

The most common form of mycorrhizal symbiosis is that of the arbuscular mycorrhizal (AM) (Smith and Read 2008) association which can form on c. two-thirds of all land plant species. The key function of the AM symbiosis is to enhance nutrient capture for the associated host plant while, in return, the fungus obtains a supply of carbon (Smith and Read 2008). However, unlike fungi involved in both the ecto- and ericoid mycorrhizal associations (Hodge et al. 1995; Read and Perez-Moreno 2003), arbuscular mycorrhizal fungi (AMF) have no known saprotrophic capabilities and so are unlikely to play a direct role in organic matter decomposition (see Leigh et al. 2011). The fungal hyphae can however explore a large volume of soil and acquire phosphorus (P) beyond the phosphate depletion zone that rapidly builds up around the root surface (Smith and Read 2008; Sanders and Tinker 1973) and it has been shown that the arbuscular mycorrhizal fungi (AMF) may largely take over the acquisition of P for their associated host plant (Smith et al. 2009). In addition, a key role for AMF in N cycling has recently been identified (Hodge and Fitter 2010) and some of the N captured from nutrient patches may be passed to their associated host plant under some conditions (Leigh et al. 2009; Hodge 2003a; Barrett et al. 2011; Hodge and Fitter 2010), but not others (Hodge 2003b; Reynolds et al. 2005). Plant N:P biomass ratios (g N/g P) can vary markedly, with individual measurements ranging from approximately 1–100, with an average ratio among terrestrial plant species of 12–13 in their natural field sites (Güsewell 2004).

The results from numerous studies verify that the quality, type and distribution of nutrient patches influence the way in which a plant grows and the nutrients which it acquires (see for example Cahill et al. 2010; Hodge et al. 1999b; Fitter 1994; Shemesh et al. 2010). Hodge et al. (1999a) and Robinson et al. (1999) observed the reaction of the grass species *Lolium perenne* L. and *Poa pratensis* L. to the presence of a high-quality N patch. Both species saw an increase in root-length density within the patch and a proportional increase in N uptake. It is also important to note that Robinson et al. (1999) concluded that the results are driven by context sensitivity, with the need for reactive proliferation strongly linked to the presence of inter-specific competition. These conclusions are supported by a modelling study which demonstrated a theoretical basis for the

weak affiliation in monocultures between proliferation and N capture. Williamson et al. (2001) and Linkohr et al. (2002) investigated the effect of the presence of a phosphate patch, the latter comparing directly with the results for the presence of an N patch. The different qualities of the two nutrients are reflected in contrasting responses to the N and phosphate patches: unlike in the response to a high quality N patch, an increased availability of phosphate caused an increase in primary root length and a decrease in lateral root density.

It is, however, challenging to disentangle the ecological processes driving the observations from experimental and field-based studies. In particular, the roles of environmental heterogeneity (nutrient patchiness), neighbourhood competition for resources, and the evolutionary context of root proliferation strategies, are hard to isolate.

With such a broad range of environmental factors influencing a plant's growth and so many physiological and morphological responses at a plant's disposal, modelling plant growth can be a daunting task. A number of different approaches have been taken in the past, focussing on different aspects of the problem (for example see Bever 2003, for a review of conceptual and empirical work on soil community feedback and competitor coexistence; Dupuy et al. 2010, for a review of root growth models; Vos et al. 2009, for a review of structural plant modelling).

Such different approaches help to yield insight into different areas of plant growth. For example, Cropper and Comerford (2005), coupled a mechanistic nutrient uptake model with a genetic algorithm to estimate the minimum addition of P required to meet the requirement of a 4-year growth demand of loblolly pine. They found that the amount of P required was doubled when using a low root length density input compared to that with a high root density input. O'Brien et al. (2007), created a spatially explicit model of below ground competition in plants, treating competition for space as an evolutionary game. They found that root spread can be predicted by the cost-benefit ratio for root production, and predict that in areas with no overlap root growth should match resource availability, whilst in areas of overlap they are predicted to display the 'Tragedy of the Commons' (Hardin 1968).

Overview of model

The aim of this work is to elucidate the processes driving root proliferation strategies by considering an idealised model of plant growth and competition in one spatial dimension. The growth of individual plants is modelled in a patchy nutrient environment, where both the quality and statistical distribution of immobile nutrient patches were known. The environmental scenarios included in this work represent plant growth with a growth limiting, fixed, immobile nutrient (such as P), requiring an individual plant to grow to it in order for acquisition, with no diffusion or movement of any other kind modelled. It is assumed that an individual plant can change its root proliferation only in response to local (temporally and spatially) information.

An idealised representation of mycorrhizal networks is then developed by grouping nutrient patches into "networks". Upon encountering a patch, a probabilistic choice is made by the plant to either acquire the individual patch, or to "join" the network and gain access to all patches within the network, albeit at a cost given that AMF are large sinks for plant assimilate (Johnson et al. 2002; Hodge 1996). Defining networks in this way, as a collection of connected patches, is an abstraction from reality (for example see Southworth et al. (2005) for a network theory analysis of mycorrhizal/plant networks), but this deliberately simplified approach allows the interplay between plant competition and mycorrhizal network dynamics to be assessed using a minimal set of assumptions, and also captures plant growth in heterogeneous environments in a way which is computationally tractable.

The basic model is simple and strategic, aiming to identify and broadly quantify the factors driving proliferation and competition in heterogeneous landscapes. Complexity is added to the model systematically. First the optimal proliferation response for an individual plant growing in isolation is obtained, in both a uniformly random and a statistically patchy environment, to show how spatial heterogeneity influences proliferation strategy. These baseline results are then compared to those arising from competition simulations (under the same average conditions). Finally the role of

mycorrhizal networks with varying spatial structures is investigated.

Whilst in a given scenario a certain strategy may achieve the greatest fitness "on average", within an evolutionary context this may not be the strategy that best enables an individual to succeed against competitors (Currey et al. 2007). By coupling the model with a genetic algorithm (GA), it is possible to find the best strategy taking into account stochasticity within the environment (resource distribution), the neighbourhood (location of competitors), mycorrhizal network structure (where applicable) as well as evolution (population dynamics, selection and mutation). Such an approach therefore facilitates assessing fitness against evolutionarily relevant metrics rather than simple mean-field properties (Currey et al. 2007; James et al. 2010; Preston et al. 2010).

For an isolated plant in a uniformly random environment, a proliferation strategy driven by encountered nutrient patches should provide on average no advantage/disadvantage, since statistically any other given patch is equally likely to be found anywhere in the environment. However, when patches are distributed heterogeneously, finding a patch provides statistical information that the next patch is likely to be close by. Consequently, one might expect that a bias toward proliferating in the direction of the last found patch would statistically be beneficial in terms of maximising exploitation of the environment per unit growth.

In the presence of competition it is less clear what behaviour will be evolutionarily favoured; in a random environment the acquisition of a patch provides information that the individual is growing, at least in the short term, into unexploited soil. As such, the plant gains indirect information about its neighbours which could in principle be beneficially exploited. Within a patchy heterogeneous environment the acquisition of patches similarly provides indirect information about the relative proximity of neighbouring plants, but also provides statistical information about the location of other patches (at least in unexploited soil). It is not clear what effect this will have on the strength of the proliferation response in comparison to the control experiments, and the GA framework developed here provides a rigourous

mechanism through which such questions can be answered.

When mycorrhizal networks are introduced, it is expected that as the cost of acquiring resources from the networks increases, the propensity for an individual to join the networks will decrease. Similarly, it is likely that responsive proliferation will become more important as the benefit from joining the networks decreases. What is not clear is what impact the spatial properties of the networks will have on when this "switch" occurs, and how it depends on the structure of the network itself.

Methods

Running in Matlab, the central model is conceptually simple: a growing plant proliferates roots in a one-dimensional patchy nutrient environment and receives a growth benefit from the acquisition of nutrient patches. This methodology is simplistic, but it is argued below that it captures the essential ingredients and allows biological, ecological, and evolutionary factors to be isolated (Table 1).

Environment

The environment ($[0, d]$ on a horizontal axis, where $d = 1$ for an isolated individual, and scaled to $d = P$ for a population of P plants) contains a series of identical, discrete nutrient patches of point physical size (i.e. negligable physical size) and quality p. The quality of a patch reflects the marginal benefit to a plant from its acquisition (see Plant Growth subsection), with

$$p = p_{tot}/n, \tag{1}$$

where p_{tot} is the (specified) expected total nutrient content and n is the (again, specified) expected number of patches in the environment. Changes in p_{tot} and n therefore allow for environments with different quantities and/or qualities of nutrient patches to be defined. For consistency across the various simulations, as well a scaling the physical size of the environment, mean nutrient content and mean patch numbers are scaled on a patches per-plant (ppp) basis. For computational

Table 1 Table of parameters used in the models

Name	Property	Value	Dimensions
α	Proliferation bias	[−1, 1] (variable)	–
β	Network preference	[0,1] (variable)	–
L_0	Initial maximum size	0.2	Mass
L_{max}	Maximum size at time t	Variable	Mass
P	Number of plants	1 (cont) 100 (comp)	–
p_{tot}pp	Mean total nutrient per plant	Fixed variable	Mass
p	Individual patch quality	Fixed variable	Mass
n	Mean no. of patches per plant	Fixed variable	–
N	No. of patches obtained by individual	Variable	–
g	Growth rate	0.5	Mass/time
dt	Time step	10^{-3}	Time
d	Size of environment	1 (cont) 100 (comp)	Length

"Variable" implies parameter takes no fixed value (detailed in text), "fixed variable" means parameter takes different fixed values in different simulations (described in text) and "cont" and "comp" refer to control and competitive environments respectively

simplicity and to avoid boundary artefacts, the environment is taken to be periodic (i.e. circular).

Two methods of patch distribution are considered, differing in the statistical properties of the distribution of the distance x between patches:

Random nutrient distribution

In this case, n nutrient patches are independently distributed uniformly randomly throughout the environment. That is, each patch is placed independently according to a uniform distribution across the entire environment. The existence of a patch at a given location therefore contains no information about the locations of other patches. Throughout this work these environments will be referred to as "random environments".

Heterogeneous nutrient distribution

Here a Pareto distribution (specifically, a non-standard Pareto distribution of the second kind; see Johnson et al. 1994) is sampled to generate inter-patch distances, x, with the probability density function given by

$$f(x) = \frac{ra^r}{(a + x)^{r+1}}, \ (x > 0). \tag{2}$$

Reparameterising the Pareto distribution (as in James et al. 2005) by letting $a = \frac{r-1}{\lambda}$, it is possible to have two parameters, λ and r, which independently define the mean distance between

patches and the "patchiness" of the overall distribution respectively. Starting at a random point, patches are placed across the environment spaced according to independent samples of these inter-patch distances. This results in an expected total of $P\lambda$ patches distributed heterogeneously across the interval $[0, d]$. Throughout this work, the parameter r remains fixed at 2.1 in order to generate heterogeneous environments whilst maintaining a finite variance in the Pareto distribution, whilst λ, which is equal to the expected number of patches per unit length, is varied to change the density of patches.

The choice of a Pareto distribution allows truly "patchy" environments to be generated, with individual patches aggregating into larger patches, and areas containing little or no nutrient emerging. Unlike in random environments, with this method the position of one patch provides statistical information about the location of neighbouring patches. Throughout this work these environments will be referred to as "heterogeneous environments". Figure 1 illustrates examples of both random and heterogeneous distributions.

Mycorrhizal networks

The networks are defined according to three different sets of rules. The first method is random (Fig. 2a), with each patch independently, randomly assigned to one of 10 networks. The second
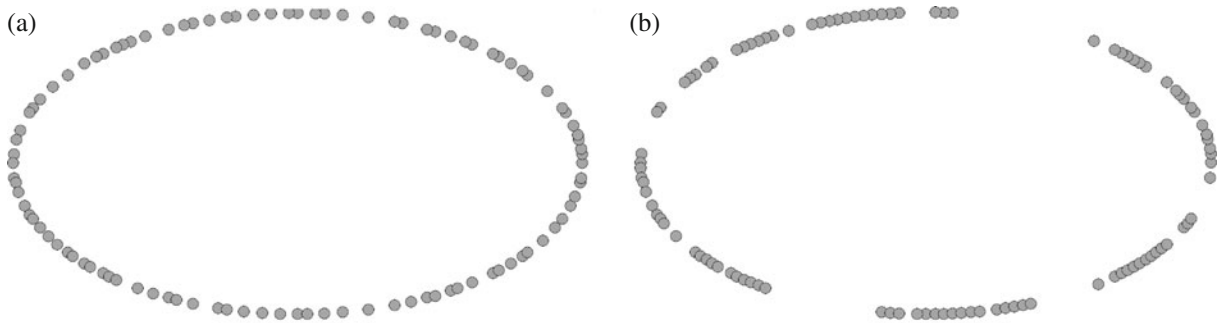
Fig. 1 Visual representations of examples of random **a** and heterogeneous **b** environmental resource distributions. Here 100 patches are distributed across the entire environment according to the two different methods

method uses a threshold parameter determined to provide on average 10 networks, where a patch lying within this threshold distance of a neighbour will belong to the same network as this neighbour, resulting in spatially-local networks (Fig. 2b). The random and local networks are at the extremes of the spectrum of possibilities, suggesting totally

uncorrelated spatial structure on the one hand, and strictly local interactions on the other. To bridge the gap between these extremes, the local networks were subjected to a small amount of random "re-wiring" (Fig. 2c). This is achieved by each patch having a 0.001 chance of selection, with selection meaning every patch in the same network
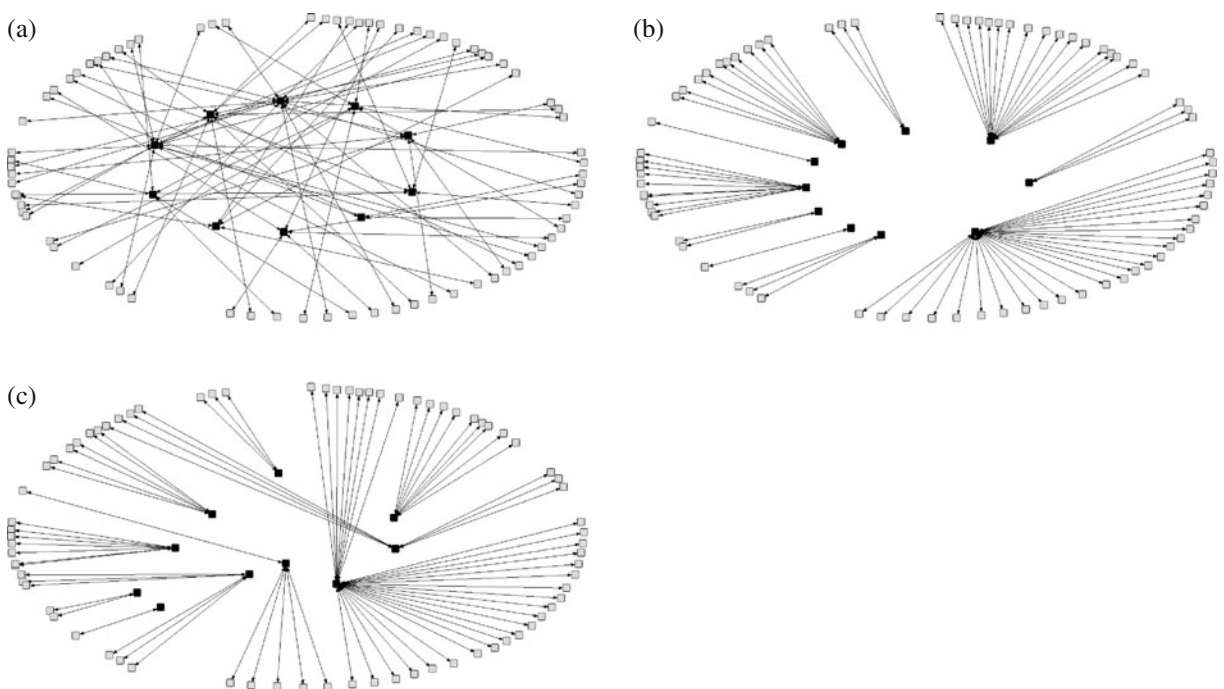
Fig. 2 Representative examples of **a** random, **b** local and **c** "rewired-local" networks in a heterogeneous nutrient environment. The *black nodes* represent the individual networks, whilst *grey nodes* represent the nutrient patches.

The location of black network nodes are purely for visual clarity, whilst relative patch positions are represented by the distribution of the grey patch nodes

after the selected patch (inclusive) being assigned to another randomly chosen network. These generalised network structures allow the complexities involved in spatially extended plant-mycorriza interactions to be captured qualitatively without the need for the extra assumptions and complications required by a fully spatially explicit model.

Plant growth

For the purposes of this study, a plant's size, L, is regarded as equivalent to the size of its root system. Mass and length are interchangable as interpretations of size of an individual within the model, but here size shall be considered as mass. The plants are independently distributed uniformly randomly throughout the environment, and growth is assumed to occur at a constant rate, g, reflecting an unmodelled background homogeneous nutrient resource. Growth is initially uniform, with proliferation equal in both directions around the environment away from the "centre" of the plant. The choice of g is arbitrary and has no impact on the outcome of the model provided suitably small time steps are implemented (i.e. provided the amount of growth in a given time step, $g * dt$, is sufficiently small). If a plant encounters a nutrient patch, then the plant experiences a rapid (instantaneous) additional growth equal to the quality of the patch, p (Eq. 1). Hence at time t, the plant is of size $L(t) = gt + N(t)p$, where $N(t)$ is the number of patches acquired by the individual at time t. The plant grows until it reaches a maximum size, L_{max}, which is dependent on the quantity of nutrient acquired with $L_{max}(t) = L_0 + N(t)p$ where L_0 is an arbitrary initial maximum size limit which can be thought of as representing a level of nutrient in the seed (fixed at 0.2 throughout this work for all individuals). Too small a value of L_0 would make it unlikely that an individual would reach an initial patch, whilst too high would make it likely an individual would easily exploit the environment. Consequently the value of $L_0 = 0.2$ is chosen as a suitable middle-ground within the confines of the rest of the model.

Previous work has shown that this method of modelling growth can be used as an accurate characterisation of a Gompertz growth function (as used by Purves and Law 2002; Lv et al. 2008) with

upper size limit equal to $L_{max}(t)$. It follows that the final size of an individual is $L = 0.2 + Np$ where N is the total nutrient acquired by the plant upon reaching its size limit. The final size of the plant is therefore a measure of the quantity of nutrient it has obtained, and is assumed to be a measure of its fitness and growth success.

Directional proliferation

When a plant encounters a patch, it is possible for the individual to proliferate roots directionally so as to potentially more efficiently exploit its environment. In order to minimise assumptions about a plant's ability to detect and "remember" its environment, a plant's information of the environment is limited to knowing in which direction its last acquired patch was located. A simple trait then uses this information, with each individual possessing a dimensionless parameter α between -1 and 1 which linearly dictates which proportion of its growth it proliferates in this direction, with a positive value representing a bias of growth towards the last found patch and a negative value resulting in a bias away. The parameter α is fixed for each individual, and is allowed to evolve between generations.

Growth with mycorrhizal networks

When the model is run for plants grown in the presence of mycorrhizal networks, expected nutrient per plant, p_{tot}pp, is fixed at 0.4 and expected patch numbers at 25 ppp. The decision to join a network is governed by a second dimensionless trait parameter, β, which takes value between 0 and 1 and equates to the probability that the plant will join the network at a given patch encounter. If the plant does join the network then it gains access to all patches within the network, with a "cost" parameter, c, determining the proportion of benefit the plant loses relative to if it were to acquire each patch independently of the network ($c = 0$ results in no cost; $c = 1$ implies full cost, i.e. no marginal benefit to the plant from acquiring resources from a network). The values of c tested were: 0.5, 0.8, 0.9, 0.95, 0.99 and 0.999. Whilst only one nutrient is explicitly modelled, the cost can be considered as a carbon cost to

the plant in an exchange process whereby all P is obtained from the network. The parameters β and c thereby efficiently characterise the trade-off between gaining full access to local nutrients, and gaining access to distant nutrients (at a cost) via a mycorrhizal symbiotic association.

Population dynamics and evolution

In order to quantify the roles played by proliferation and network parameters α and β under different ecological scenarios, the model was coupled with a genetic algorithm (GA) for both "control" (individuals grown in isolation in environment size [0, 1]) and competitive (a population of 100 plants competing for available resources in environment size [0, 100]) conditions. Using the final size of an individual as a measure of its fitness, the GA allows the relative success of plants with different values of α and β to provide evolutionarily derived optimum values for a given scenario.

The GA works as follows:

1. An initial population is created with each individual possessing randomly chosen proliferation (α) and, where applicable, network (β) parameter values.
2. The model is run and these individuals are then assessed for success within the generation as defined by the fitness function.
3. The most successful are identified and the next generation is created as their offspring, inheriting their α and β values.
4. The offspring then experience small, independent, individual mutations to their inherited parameter values.
5. Return to step 2.

This cyclic process continues until enough generations have been iterated for convergence (absolute or statistical) to occur. The GA uses a truncated selection process to select the fittest 10% of individuals in a generation, with each of these individuals producing 10 cloned offspring with mutation in the subsequent generation. Mutations, defined here as small random changes to the inherited parameter values, occur with 100% probability, with the mutations sampled from a

uniform distribution with limits −0.05 and 0.05. See Supplementary Information for further details of GA choice and implementation.

Results

Proliferation reponse for isolated plants, and plants in competition

The evolved mean values of the proliferation parameter α are shown in Fig. 3, with bars indicating the variability in the outputs of the evolutionary algorithm. Explicitly, for each evolutionary simulation, we subsample at 1,000 generation intervals so as to arrive at 100 pseudo-independent samples. Autocorrelation analysis establishes that this interval is sufficient for subsamples to be treated as statistically independent (see Supplementary Information for details). The bars show the standard deviations for these subsamples. Treating the data as independent samples, significant differences in the mean from value 0 can be established by a t-test, indicated by the standard * notation. Results are shown for different permutations of patch numbers and total nutrient content, for control and competitive environments, and with random and heterogeneous patch distributions. These results summarise the long term averages of trait distributions across the modelled populations.

As anticipated, regardless of nutrient levels and patch density, the individuals grown in control tests within randomly defined environments demonstrate no proliferation preference (α remained close to 0).

In contrast, an isolated individual grown in a patchy heterogeneous environment demonstrates a propensity to proliferate towards the last found patch ($\alpha > 0$), though the value of α depends on patch density and, to a greater degree, global nutrient levels. In particular, at high nutrient levels and low patch density (Fig. 3c) there is no signal for a proliferation strategy.

In random environments, the introduction of competition causes a shift from no benefit in proliferation strategy to a preference to proliferate towards the last found patch ($\alpha > 0$). This demonstrates that the presence of competition allows

Fig. 3 Evolved mean values for proliferation preference, α, for plants grown in random and heterogeneous environments, in isolation (control) and among neighbours (competition). All tests were run for 5 (**a** and **c**) and 25 (**b** and **d**) patches per plant (ppp), and nutrient levels of p_{tot} equal to 0.2 (**a** and **b**) and 0.8 (**c** and **d**) per plant (p_{tot}pp). The *bars* show the standard deviations of 100 uncorrelated sub-samples from each simulation, see text for details
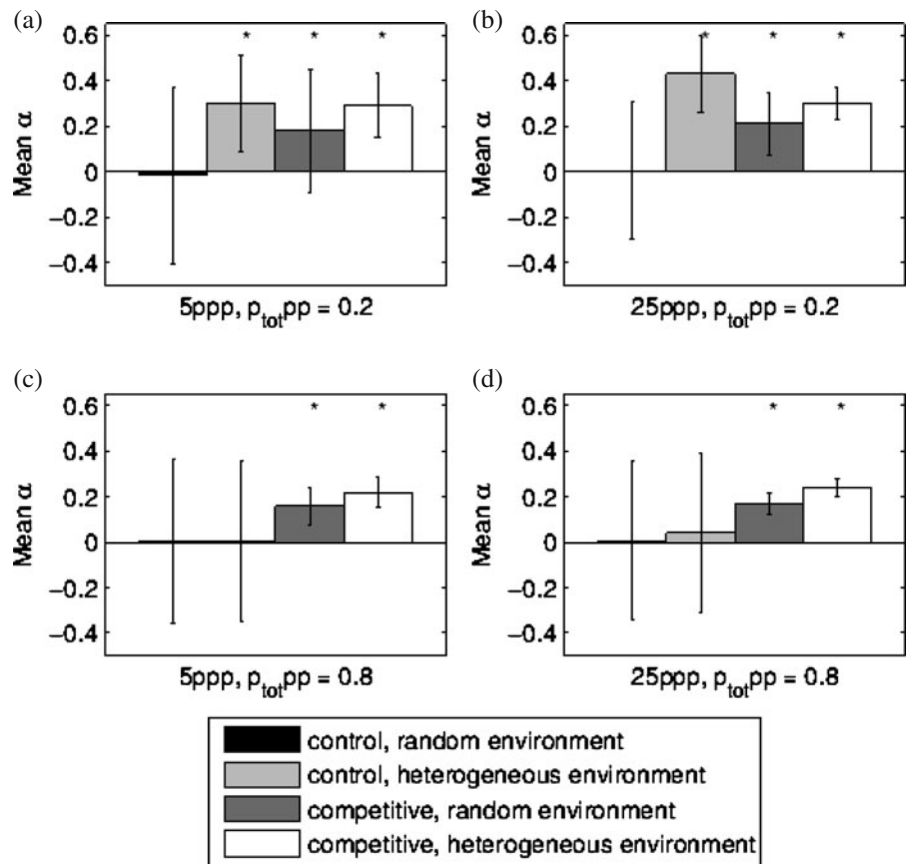
an individual to improve its relative ability to exploit its environment by responding to encountered patches, even without any implicit statistical information about the environment.

At high nutrient levels, the introduction of competition in patchy heterogeneous environments causes an increased propensity to proliferate towards the last found patch (Fig. 3c and d). However, at lower nutrient levels where the control tests provide a strong signal for a positive α value, a weakening of the signal and a reduction in the benefit of possessing a positive proliferation value is observed (Fig. 3a and b).

With the exception of isolated individuals in random environments (where no proliferation strategy ever emerges), all results show that a higher patch density results in an increase in proliferation toward the last found patch (Fig. 3b and d). In contrast, at high nutrient levels there is a reduction in necessity to proliferate in such a way (Fig. 3c and d).

Additional heterogeneous control tests

In order to investigate the observed dependence on patch numbers and nutrient levels, further control tests within patchy heterogeneous environments were carried out for a larger set of nutrient levels (p_{tot}pp ranging from 0.05 to 0.8 in 0.05 increments) and a greater range of patch numbers (5, 10, 25, 50, 100 and 250 ppp). Figure 4 summarises the results from these tests, with standard deviations omitted for clarity (see Supplementary Information for details).

At low patch numbers, proliferation response to patches (α) remains at a positive value as the total nutrient level increases, before beginning to decrease as the total nutrient content is further increased. This continues until α settles around 0.

As the number of patches increases (and accordingly individual patch quality decreases by Eq. 1), both the rate at which α converges to 0 and the nutrient level at which this transition occurs

Fig. 4 Evolved mean values for proliferation preference, α, plotted against expected nutrient levels per plant (p_{tot}pp) for isolated individuals grown in heterogeneous environments. Expected patch numbers are: 5, 25 and 250 patches per plant (ppp). Standard deviations omitted for clarity (see Supplementary Information for more details)
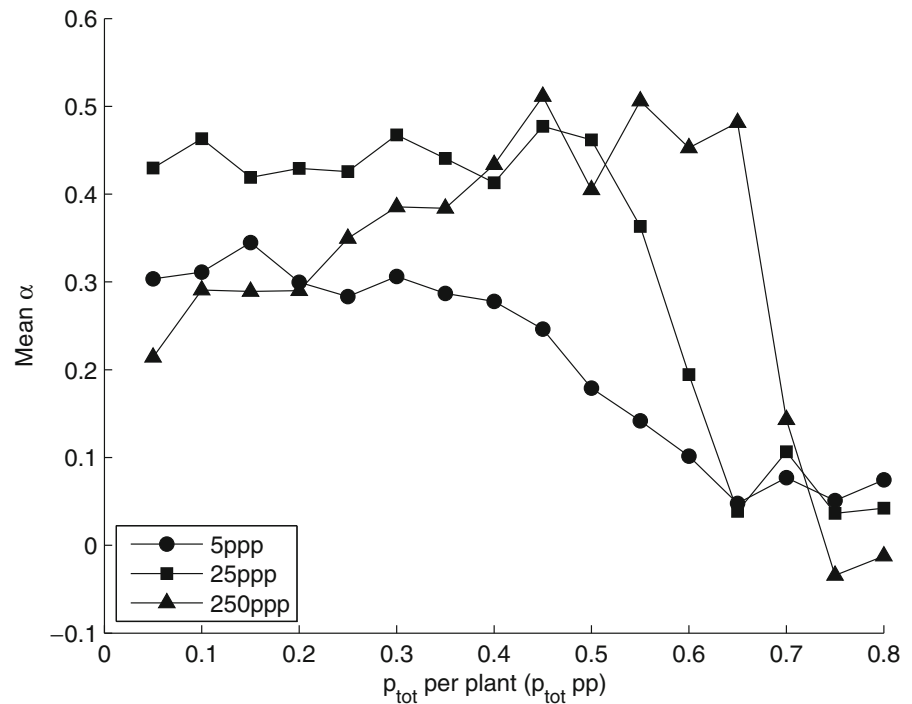
are seen to change. With increased patch numbers, the transition takes place over a smaller range of nutrient levels (i.e. a steeper descent), and the transition occurs at higher nutrient levels. As well as these qualitative and quantitative changes to the observed transitions, with increasing patch numbers there is a lowering of the mean α value at lower nutrient levels.

From the lowest mean patch number (5 ppp) to the highest (250 ppp) tested, the evolved response of the proliferation bias, α, to an increase in total nutrient content shifts from steadily reducing and converging to value 0, to increasing steadily before sharply dropping to a value of 0. The results for 10, 50 and 100 ppp are consistent with these trends but are omitted from Fig. 4 for clarity.

Proliferation and symbiosis responses for plants grown in competition in the presence of mycorrhizal networks

Figure 5 summarises the results for tests with competition in the presence of mycorrhizal networks. Figure 5a shows the effect of cost on

proliferation strength (α) for different network types, and Fig. 5b shows the effect on propensity to join the network (β). Results are plotted against a rescaled cost $-\log(1 - c)$; this rescaled cost increases monotonically with c, and the logarithm form allows a wide range of c values to be displayed.

In general (irrespective of network type) at relatively low cost to acquiring resources through the networks (small c value) there is no foraging preference (α remains close to 0) (Fig. 5a) and a preference to join the network ($\beta > 0.5$) (Fig. 5b). As the relative cost of acquiring resources from the network is increased ($c \rightarrow 1$), there is a switch from a plant's growth being driven by network symbiosis to being proliferation oriented, with it becoming less desirable to join the networks ($\beta \rightarrow 0$) and foraging strategy becoming relevant with a positive preference to proliferate towards the last acquired patch ($\alpha > 0$).

The propensity to join the random mycorrhizal networks at lower cost (c) is less than for the other types of mycorrhizal networks. As c increases, this propensity also increases, and carries on doing so past the cost at which under other network types

(a)

(b)
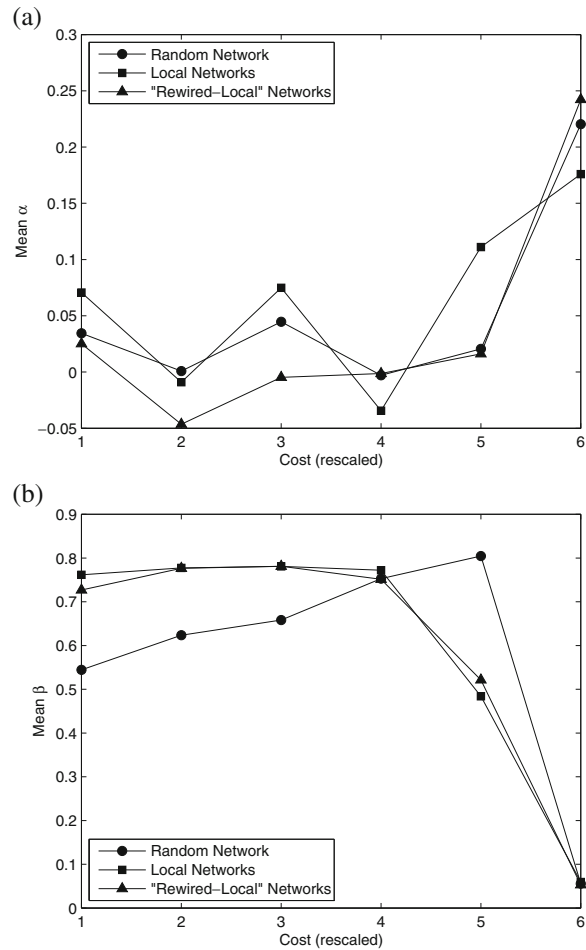
Fig. 5 Plots of evolved mean **a** proliferation preference, α, and **b** propensity to join a network, β, values. Plotted against rescaled cost $-\log(1-c)$, where c is the network associated cost (see text for details), for different network types. Standard deviations omitted for clarity (see Supplementary Information for more details)

a shift in preference for precision over symbiosis occurs.

Discussion

Comparing results (Fig. 3) from the control tests in random and heterogeneous environments demonstrates that no benefit exists from proliferating in response to patch acquisition when the acquisition of a patch provides no information about the environment. When the patches do provide information, this can be used to an individual's advantage by directing proliferation in response to acquiring the patch.

As would be anticipated, exceptions occur to this pattern when global nutrient levels are too low or too high (Figs. 3c and 4). As patch quality tends towards zero, so too does the relative benefit of acquiring a patch, and thus the potential reward for proliferating in response to the presence of patches. If p is large enough, the relative benefit from finding such a patch becomes so great that there is no longer a need to be selective in proliferation, despite the increased reward in obtaining the undiscovered patches.

The contrasting results for control and competitive tests (Fig. 3) within random environments confirm that, in the presence of competition, finding a patch imparts useful information to

a plant. This is true even in an environment where a single patch provides no information about the distribution of the remaining patches. With no signal of neighbour presence/proximity contained within the model, an individual can never know that it is overlapping with a competitor and therefore proliferating into exploited soil. However, the acquisition of a patch does inform an individual that it is not at that moment overlapping with such a competitor. Information that proliferation in a given direction is definitely not in a region of overlap provides a strong enough advantage to bias growth in this direction.

In patchy heterogeneous environments where an individual patch potentially contains information about both the unexplored environment and also the presence (or, more precisely, absence) of competitors, a slightly more complicated picture emerges. References to control tests show that within a heterogeneous environment the strength of signal for a positive trait, when it exists (Fig. 3a and b), often decreases with the introduction of competition. Conversely, where little or no signal exists (Fig. 3c and d), the addition of competition leads to the emergence of a positive trait value. This, together with the results for the additional heterogeneous control tests (Fig. 4), demonstrates that competition could reduce the effectiveness of responding to patches within low-mid nutrient level environments, but in nutrient rich environments could provide an additional pressure that necessitates selective proliferation. Further, the greater α values from heterogeneous competitive environments compared to random competitive environments demonstrates that not only can the addition of competition cause a positive signal to emerge, but part of this signal represents the emergence of a benefit in responding to the patch distribution.

Hodge et al. (2009) observed that not all plants respond in the same way to self/non-self competition (see also Hess and de Kroon 2007; Schenk 2006; Masclaux et al. 2010; Milla et al. 2009). With no ability for an individual to directly detect neighbours, and the plants represented in this work being non-species specific, there was no scope for "kin" or competitor recognition (see for example, Dudley and File 2007; Bhatt et al. 2011; Murphy

and Dudley 2009) and evolutionary selection pressure applies only at the individual level in the model.

However, the results shown here provide theoretical support for experimental results seen for particular species. Cahill et al. (2010) found that for *Abutilon. theophrasti* seedlings grown alone and in competition, in treatments combining different levels of resource heterogeneity, that root placement was driven by a "hierarchical set of decision rules dependent on presence or absence of a neighbour". As in the results shown here at high nutrient levels (Fig. 3c and d), regardless of resource heterogeneity, in isolation a plant would grow with a broad foraging strategy ignoring the resource distribution. In the presence of competitors, a more specific foraging strategy was adopted and was modified by resource distribution. More broadly, Cahill et al. (2010) conclude that plants "non-additively integrate information about both resource and neighbour based cues in the environment", which is consistent with the evolved results presented in this work.

When mycorrhizal networks were introduced, the general pattern of behaviour was easy to understand. At relatively low costs for acquiring resources via the networks (low c value) the plant had a strong pressure to join the networks. This is shown both by a propensity to join (large β value), but also by the lack of signal for a positive proliferation (α) value. Effectively a plant needed to join the networks in order to be successful, and consequently proliferation strategy became insignificant. As the cost increased, a point was reached where it no longer remained beneficial to the plant to join the network, and so β decreased to 0. At the same time, root proliferation became important again, hence the emergence of a signal for a positive α value.

At lower costs, the reduced pressure (lower β value) to join random networks compared to local and "rewired-local" networks does not reflect a relative lack in benefit in doing so, either directly to the individual or indirectly by depriving neighbours of resources. One explanation for the observed reduction in β could be that at such low costs, there was only scope for such a small number of individuals to monopolise the networks/ resources that within the GA the selection

pressure did not get fully expressed when using a truncated selection method.

Within an environment of random networks, the benefit to an individual from joining a network resulted in greater potential to join subsequent networks than with local and "rewired-local" networks. This made it possible for an individual to monopolise not only local resources, but also those over a greater spatial range. Consequently, there was greater potential to deprive the competition of available resources than with spatially structured networks. This explains why it was beneficial to continue joining the networks and resist switching to a proliferation-based growth strategy when the cost of doing so would have suggested otherwise. The lack of difference between results for local and "rewired-local" networks suggest that not enough rewiring took place to make a significant difference. With increasing amounts of rewiring the networks would tend towards random networks, suggesting a greater level of rewiring than was performed would see results in between those of the random and local network tests.

As discussed in the introduction, the implementation of mycorrhizal networks was necessarily idealised due to constraints imposed by the original model. Within such a framework, it was impossible to implement many of the dynamic features of plant/network interactions (Smith and Read 2008; Hausmann and Hawkes 2009). As such, this implementation acted to demonstrate the significance of the spatial distribution of networks among plants/resources on the cost/benefit relationship between plants and networks, and to inform future experiments and their research. The limitations also highlight the need for moving into a more temporally explicit model. Such a model would also allow the order of patch encounter (Duke and Caldwell 2000), temporal network dynamics (Hausmann and Hawkes 2009), and the physical size and temporal properties of patches (Fitter 1994; Hodge 2004) to be integrated.

Also, although it is recognised that roots can also modify their environment and the microbial decomposing community through rhizodeposition processes (Paterson 2003; Paterson et al. 1999; Hodge et al. 1998b; Kuzyakov 2002) this was not included in this model not least because rhizode-

position itself can be affected by many environmental factors (Hodge and Millard 1998; Hodge et al. 1997, reviewed by Jones et al. 2004, 2009; Hinsinger et al. 2009), and thus is often difficult to quantify.

The model is restricted to growth in one spatial dimension, but one can argue that the evolutionary effects on proliferation strategies will be amplified in higher dimensions. In one dimension, local proliferation in the "correct" direction happens 50% of the time when growth is random, and any evolved strategy can only improve upon this. In higher spatial dimensions there are more "incorrect" possible growth directions, and so the relative advantage of a directional proliferation strategy is increased. Similarly, as the number of dimensions is increased, so too is the complexity of the spatial distribution of patches. Consequently, a trait which maximises proliferation efficiency and allows more precise exploitation of space stands to be more beneficial in higher dimensions. As such, it is reasonable that the selection pressure to possess and utilise such a trait will be greater in higher dimensions and that a stronger signal would emerge for a parameter governing such behaviour. However, extension of the simulations to higher dimensions requires further assumptions, and is not considered here.

Robinson et al. (1999) suggested for a highly mobile and diffusive nutrient like N that it is the presence of inter-specific competition that drives the benefit for responsive proliferation. In that scenario, the mobility of the nutrient makes it unnecessary for the plant to be particularly selective in its proliferation of roots, but the added pressure of competition provides the benefit from response to the environment. The results presented here show that similar evolutionary forces can drive the emergence of reactive proliferation in response to randomly distributed immobile nutrients in environments where isolated plants do not benefit from such behaviour. With no direct information imparted to an individual about the presence and proximity of competitors in this model, the acquisition of immobile nutrient patches provided enough information for a plant to gain, on average, an advantage by responding to them, regardless of their distribution or quality.

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