Oecologia (2012) 170:925–933
DOI 10.1007/s00442-012-2358-0

BEHAVIORAL ECOLOGY - ORIGINAL RESEARCH

Context dependence in foraging behaviour of *Achillea millefolium*

Justine D. Karst · Pamela R. Belter · Jonathan A. Bennett · James F. Cahill Jr.

Received: 17 October 2011 / Accepted: 1 May 2012 / Published online: 24 May 2012

Abstract Context-dependent foraging behaviour is acknowledged and well documented for a diversity of animals and conditions. The contextual determinants of plant foraging behaviour, however, are poorly understood. Plant roots encounter patchy distributions of nutrients and soil fungi. Both of these features affect root form and function, but how they interact to affect foraging behaviour is unknown. We extend the use of the marginal value theorem to make predictions about the foraging behaviour of roots, and test our predictions by manipulating soil resource distribution and inoculation by soil fungi. We measured plant movement as both distance roots travelled and time taken to grow through nutrient patches of varied quality. To do this, we grew *Achillea millefolium* in the centers of modified pots with a high-nutrient patch and a low-nutrient patch on either side of the plant (heterogeneous) or patch-free conditions (homogeneous). Fungal inoculation, but not resource distribution, altered the time it took roots to reach nutrient patches. When in nutrient patches, root growth decreased relative to homogeneous soils. However, this change in foraging behaviour was not contingent upon patch quality or fungal inoculation. Root system breadth was larger in homogeneous than in heterogeneous soils, until measures were influenced by pot edges. Overall, we find that root foraging behaviour is modified by resource heterogeneity but not fungal inoculation. We find support for predictions of the marginal value theorem that organisms travel faster through low-quality than through high-quality environments, with the caveat that roots respond to nutrient patches per se rather than the quality of those patches.

Keywords Behaviour · Heterogeneous · Inoculation · Marginal value theorem · Roots

Communicated by Bernhard Schmid.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-012-2358-0) contains supplementary material, which is available to authorized users.

J. D. Karst (✉) · P. R. Belter · J. A. Bennett · J. F. Cahill Jr.
Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada
e-mail: justine@karst.ca

Introduction

Though science aims for general understanding, ecology tends to produce specific results contingent on organisms and environments. Over time and space, the composition of organisms and conditions in the abiotic environment changes. For an individual, this ecological "context" can be paramount in determining function and fitness. Behavioural adjustments are common responses to varied contexts, i.e. context emerges through behaviour (Gordon 2011). Identifying the context that results in behavioural shifts is critical, as it illuminates how selection may shift in time and space. Here, we address how abiotic and biotic factors interact to affect the foraging behaviour of the plant *Achillea millefolium*, a species previously documented to show optimality when responding to heterogeneity in soil resources (McNickle and Cahill 2009).

For animals, context-dependent behaviour is acknowledged and well documented. For instance, some animals alter their foraging behaviour to negotiate patchy resources (Charnov 1976) and to manage predator risk (Brown and Kotler 2004). Plants, like animals, display sophisticated foraging behaviours (Gleeson and Fry 1997; Karban 2008; Kelly 1990); however, unlike animal behaviour, the contextual determinants of plant foraging behaviour are generally

poorly understood. To date, a major focus of research on plant foraging behaviour has been to understand how roots forage for soil resources (Cahill and McNickle 2011; de Kroon and Mommer 2006; Hodge 2004; McNickle et al. 2009), which is known to vary both temporally (Farley and Fitter 1999) and spatially (Jackson and Caldwell 1993). The distribution of soil resources, however, is but one of many putatively relevant factors affecting plant behaviour. For example, the roots of most plant species engage in symbioses with mycorrhizal fungi (Brundrett 2009), which greatly alter root function (Smith and Read 2008). These soil fungi typically provide plants with soil nutrients such as nitrogen and phosphorus in exchange for photosynthate. Mycorrhizal fungi, similar to roots, are patchily distributed in the soil (Carvalho et al. 2003; Klironomos et al. 1999; Mummey and Rillig 2008) and, depending on local conditions, these fungi can be beneficial, neutral, or parasitic to their plant hosts (Hoeksema et al. 2010; Johnson et al. 1997; Klironomos 2003). Though their role as parasites has been historically de-emphasized, particular plant–fungal combinations and environmental conditions can give rise to outcomes that are detrimental to the host (Hoeksema et al. 2010; Jones and Smith 2004). In addition to mycorrhizal fungi, free-living pathogenic fungi in soils are a notable cause of poor plant performance and/or shifts in abundance, and are often implicated in negative plant–soil feedbacks (Augspurger 1983; Packer and Clay 2000). In general, the presence and composition of soil biota affects plants from the level of an individual to a community, with outcomes ranging from positive to negative for the plant (Bever et al. 2010). How soil resource distribution and soil fungi interact to affect the foraging behaviour of plants is unknown.

Studies on animals show that the behaviour of hosts can change remarkably when infected by other organisms such as parasites (Moore 1995, 2002). Notably, shifts in feeding and foraging behaviours are often observed by infected hosts (Barber et al. 2000; Barber and Huntingford 1996; Lefevre et al. 2009; Levri and Lively 1996). Mycorrhizal fungi require 4–20 % of the photosynthates produced by host plants (Grimoldi et al. 2006; Smith and Read 2008) and, like other parasites, their energetic demands represent a cost to their hosts. Mycorrhizas may also result in benefits through nutritive gain, with the net benefit ranging from positive to negative. Similarly, pathogenic fungi can reduce biomass along with a variety of other effects on plants. The idea that soil fungi affect plant foraging behaviour has been previously recognized (Hodge 2004; Tibbett 2000) and tested (Cui and Caldwell 1996; Hodge et al. 2000; Wijesinghe et al. 2001), but these studies have focused on only one aspect of plant foraging behaviour: the static spatial distribution of roots. Explicit recognition that foraging is an active process involving movement and time has been lacking.

Behaviour consists of many components beyond documenting the static spatial distribution of foraging. For instance, optimality models such as the marginal value theorem make predictions about individual foraging effort in patches and patch-leaving behaviour (Charnov 1976), which has been successfully applied to plants (McNickle and Cahill 2009). A key prediction of these models is changes in the movement of individuals, something that can only be tested with direct observations of roots. For example, patch-leaving behaviour of animals is often assessed as "giving-up time", the amount of time an animal spends in a patch before leaving. An extension of the marginal value theorem predicts that roots of plants grown in heterogeneous conditions should travel less than those grown in homogeneous soils, because roots will remain in patches that they have already found, rather than seek new patches. Such an outcome could be consistent with an active foraging response (Cain 1994). Alternatively, if roots travel more in heterogeneous than in homogeneous soils, this outcome represents a passive foraging response, i.e. their increased growth is a simple reflection of encountering resource patches. The marginal value theorem also predicts that if energy costs are increased for an individual, then the time spent in resource patches should decrease (Charnov 1976). In animal host–parasite systems, parasites have been shown to impose and even magnify foraging costs (Raveh et al. 2011). Soil fungi functioning as parasites may therefore cause roots to leave resource patches earlier than those of plants without fungal inoculum.

Here, we manipulated soil resource distributions and inoculation by soil fungi, and monitored root movement through the soil using a series of images taken belowground, allowing us to observe contextual fine-scale patterns of root foraging behaviour. Our study is the first to investigate how soil fungi may modify the in situ dynamic movement of roots. We also measured host level consequences of root foraging behaviour through plant nutrient capture and biomass produced. Our objectives were to identify whether the context, fungal inoculation and soil resource distribution, altered root foraging behaviours. We measured foraging behaviours directed at understanding the movement of roots, i.e. distance travelled, and giving-up time (sensu Charnov (1976)).

Methods

Experiment

We grew *A. millefolium* L. with either heterogeneous or homogeneous nutrient distributions, and with or without fungal spore inoculation, in a fully factorial design. Roots of *A. millefolium* are sensitive to nutrient patches (Johnson

and Biondini 2001; Rajaniemi 2007) and the presence of arbuscular mycorrhizal fungi tends to reduce the biomass of this species (Allison 2002; Smilauer and Smilauerova 2000). This species has also been used to test predictions of the marginal value theorem for root foraging behavior (McNickle and Cahill 2009).

Seed was collected from wild *A. millefolium* plants in a native mixed grass prairie at Kinsella (AB, Canada). Seeds were germinated in starter trays filled with a mixture of sand and commercial topsoil (Greenharvest Topsoil Plus) at a 3:1 (volume:volume) ratio. Upon the development of true leaves, seedlings were transplanted to experimental pots. To eliminate potential fungal contaminants, all substrates were sterilized. Soils were autoclaved at 121 °C and 138 kPa for 45 min and then re-autoclaved after 24 h. Starter trays and experimental pots were bleached for 24 h prior to their use.

The heterogeneous soil treatment consisted of a "high" and a "low" nutrient patch, while the homogeneous soil treatment was a spatially uniform environment, i.e. the nutrients present within the low and high patches were mixed evenly into the background soil (Fig. S1 of the Electronic supplementary material, ESM). At the pot level, nutrient levels were the same between homogeneous and heterogeneous soil treatments. Patch quality was manipulated by altering the ratio of sand:topsoil and steer manure (Nu-Grow IP). The volume of steer manure in high and low patches was 66 and 25 %, respectively, and the background soil was a 3:1 mixture of sand and topsoil. Soil with manure concentrations identical to the high nutrient treatment have been shown to increase *A. millefolium* biomass threefold over manure-free background soil (McNickle and Cahill 2009). Plants were grown in plastic pots of size 58 × 17 × 12 cm, which were divided into two compartments by rigid plastic sealed with silicone; a plant was grown in the center of each compartment. A clear plastic minirhizotron tube (5.7 cm in diameter, 1.8 m in length) was inserted lengthwise through a sealed hole in the plastic divider 5 cm below the soil surface of each pot to accommodate root observations for the duration of the experiment. Two experimental pots were held on each minirhizotron tube, and the four treatments, replicated twelve times, were randomly assigned to each of the four positions on a tube. Due to mortality, the number of replicates was reduced over the course of the experiment; ten plants survived per treatment combination, except for the homogeneous soils receiving fungal inoculation, which had 11 plants remaining.

Fungal inoculation consisted of adding approximately 500 spores at the time of planting, with an additional inoculation of 500 spores occurring 30 days later. Spores were extracted from trap cultures (original soil collected from Kinsella, AB, Canada) using a density gradient of water and a 60 % sucrose solution (modified from Jenkins (1964)). Fungal spores could be from a variety of nutritional types: pathogenic, saprophytic, or mycorrhizal. A visual inspection based on size suggested that the spores were predominantly arbuscular mycorrhizal, but it is possible that non-mycorrhizal spores were introduced as a by-product of the spore extraction. The trap culture soil originated from the area where seeds of *A. millefolium* were collected, thereby ensuring that the plant and fungal genotypes potentially co-occur in nature. To control for bacteria and other microbes attached to the spores, filtrate from the extraction containing particles smaller than 38 μm in size was applied to both inoculated and uninoculated plants (3 ml to each). Plants were grown in the University of Alberta, Department of Biological Sciences Greenhouses with a 16:8 light:dark cycle and watered as required. At harvest, shoots were clipped and roots were extracted and washed over a 2 mm sieve for biomass determination. Shoots and roots were then dried at 60 °C for 48 h and weighed. Shoots were then ground with a Retsch ball mill and analysed for phosphorus and nitrogen at the Natural Resources Analytical Laboratory at the University of Alberta.

In situ root foraging

Patch and plant locations were marked on the tube before the start of the experiment, and patch soil was visually distinguishable from background soil. Three transects were used for each tube, allowing the visualization of roots along the top of the tube and on either side (90° to the top transect). Using a minirhizotron camera (Bartz technology), we took images of roots in each of 16 frames (1.5 × 2 cm) along the three transects every 3–4 days over the course of the experiment. For each time period, we measured the maximum distance roots travelled across the three transects for each side (left or right) of a plant. The experiment was ended when roots of all but four plants had traveled past patches (day 63). A modified version of giving-up time for roots was calculated as the number of days until roots were observed to grow into (60 mm from the plant) and beyond (>90 mm from the plant) patch locations.

Statistical analyses

The distance roots travelled was examined as a function of soil resource distribution (heterogeneous or homogeneous), fungal inoculation, and their interaction, using repeated measures linear models with time (image session) as the repeated measure (total of 18 sessions). Roots growing towards high and low nutrient patches were compared with their equivalent locations in homogeneous soils using separate models. We tested for sphericity and corrected degrees

of freedom using Greenhouse–Geisser estimates. At the plant level, we also examined asymmetry in bilateral root growth by calculating the distance roots grew towards the high nutrient patch minus the distance roots grew towards the low nutrient patch. Asymmetry as a function of soil resource distribution, fungal inoculation, and their interaction were tested using a linear mixed model with these factors as fixed effects and tube identity as a random effect.

How long it took roots to approach and grow beyond a patch location was tested in two separate models corresponding to observations for the two different positions. Each mixed model was constructed with plant identity as a random effect and fungal inoculation, soil resource distribution, and their interaction as fixed effects. We treated plant as a random effect in these models because in some cases patch-leaving behaviour was assessed in patches for both sides of the plant. We followed this analysis with another that examined how patch quality (low or high nutrients) in heterogeneous soils affected giving-up times. Models included fungal inoculation, patch quality, and their interaction as fixed effects for time taken to reach and grow beyond nutrient patches.

For plant-level measures (root to shoot ratios, and ln-transformed total, shoot, root mass, and shoot concentrations of N and P), we used linear mixed models with fungal inoculation, soil resource distribution, and their interaction as fixed effects, and tube as a random effect for analyses. For all models, normality was assessed by visual inspection of residuals. All analyses were performed in PASW statistics v.18.0.0 (SPSS Inc., 2009, Chicago, IL, USA). Mean ± 1 SE are presented.

Results

Distance travelled by roots

Between days 25 and 49, roots travelled further from plant stems in homogeneous than in heterogeneous soils when roots were growing towards a high-nutrient patch (resource distribution: $F_{3.98,147.28} = 3.099$, $P = 0.018$) (Fig. 1). On day 49, root growth between the two treatments converged as roots approached the edge of the pots (100–120 mm). When growth was towards low-nutrient patches, there was no difference in distance travelled between homogeneous and heterogeneous soils (resource distribution: $F_{4.07,150.57} = 0.941$, $P = 0.443$). Fungal inoculation had no significant effect on the distance roots travelled, regardless of patch quality (minimum $P > 0.06$). At the plant level, asymmetry in bilateral root growth was not affected by any treatments (minimum $P > 0.15$) (Table S1 and Fig. S2 of the ESM). Root growth on the right side was positively correlated with that on the left side of the plant (Pearson $r = 0.570$; $P < 0.01$) (Fig. S3 of the ESM).

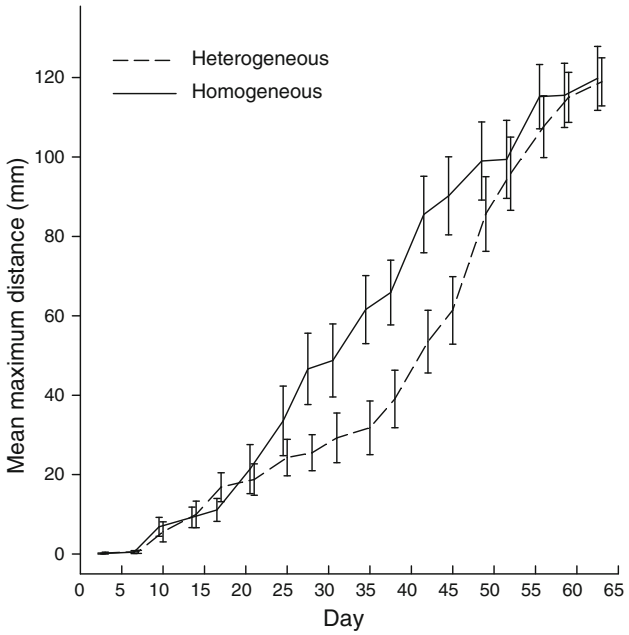

Fig. 1 Distance travelled by roots of *Achillea millefolium* over time in two soil resource environments. Values are mean ± SE; $n = 20$ (heterogeneous) and $n = 21$ (homogeneous)

Giving-up times for roots growing through nutrient patches

Fungal inoculation ($F_{1,46} = 11.62$, $P = 0.001$) but not the soil resource distribution ($F_{1,46} = 1.46$, $P = 0.233$) altered the time it took roots to reach nutrient patches or their corresponding locations in homogeneous soils. Fungal inoculation tended to slow root growth (Fig. 2a). The time it took roots to move beyond patch locations depended on the soil resource distribution ($F_{1,39} = 4.54$, $P = 0.039$) and not fungal inoculation ($F_{1,39} = 1.436$, $P = 0.238$). Roots stayed longer in patch locations in heterogeneous soils (Fig. 2b). When patch quality was taken into account for roots growing in heterogeneous soils, fungal inoculation still affected the time for roots to reach nutrient patches ($F_{1,24} = 7.596$, $P = 0.011$), but whether the patch was of low or high nutrient quality had no effect ($F_{1,24} = 0.912$, $P = 0.349$). Neither fungal inoculation ($F_{1,28} = 0.166$, $P = 0.687$) nor patch quality ($F_{1,28} = 0.857$, $P = 0.362$) had an effect on the time for roots to grow beyond nutrient patches.

Plant-level responses

Total biomass was less with fungal inoculation than without (Fig. 3a). Neither soil resource distribution nor its interaction with fungal inoculation had a significant effect on plant biomass (Table 1). The same trend was evident for shoot and root mass (data not shown). Root to shoot ratios

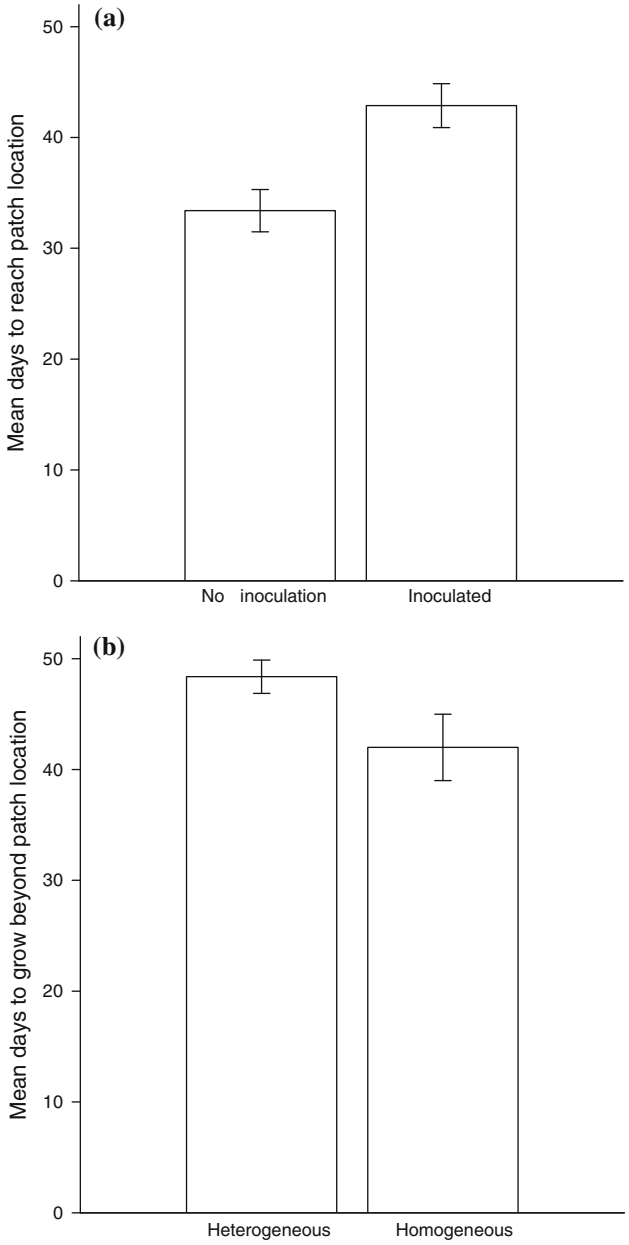

Fig. 2 Mean number of days (±SE) for roots of *Achillea millefolium* to **a** grow into patch locations (6 cm from stem of plant) ($n = 50$) and **b** grow beyond patch locations (>9 cm from stem of plant) ($n = 43$) in response to **a** fungal inoculation and **b** soil resource distribution. Untransformed data are presented; analysis was performed on ln-transformed values

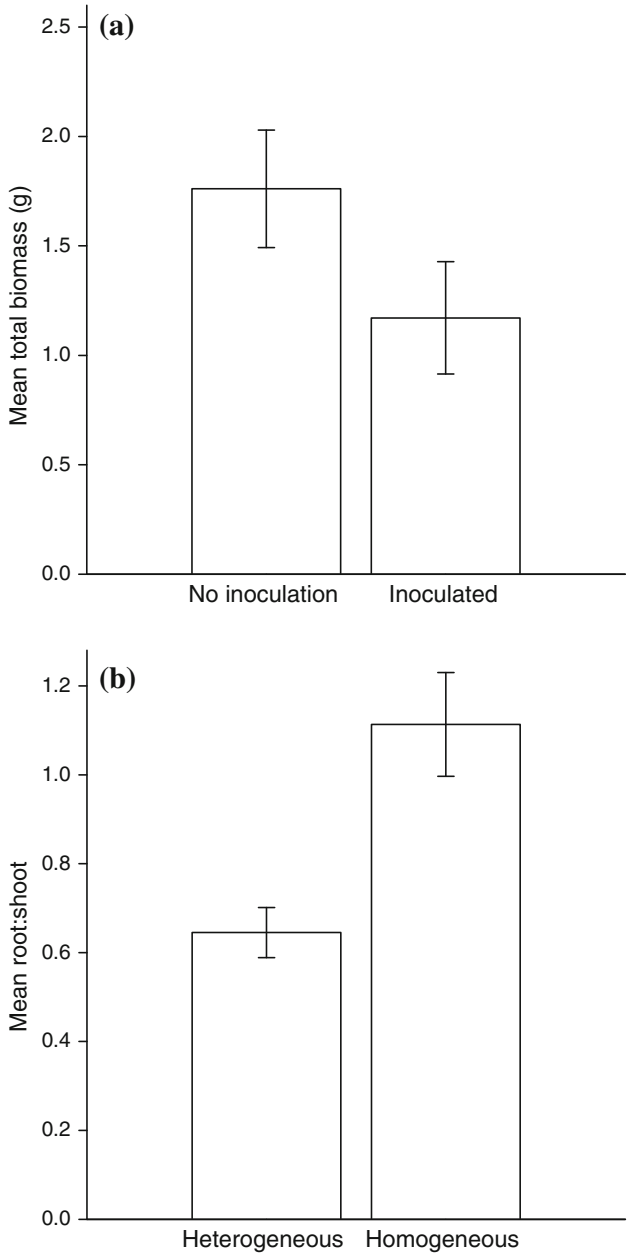

Fig. 3 **a** Total biomass and **b** root to shoot ratios of *Achillea millefolium* in response to the soil resource distribution. Untransformed data are presented; analysis was performed on ln-transformed values. Values are mean ± SE; $n = 20$ (heterogeneous) and $n = 21$ (homogeneous)

decreased by nearly half in heterogeneous soils (Fig. 3b), but were unaffected by fungal inoculation (Table 1). Fungal inoculation was associated with an increase in shoot phosphorus concentration (Table 1; Fig. 4a). There was a marginally significant interaction between fungal inoculation and the soil resource distribution, suggesting that the difference in plant N content only occurred in the absence of inoculation (Table 1; Fig. 4b).

Discussion

Context dependence in the foraging behaviour of plants has been recognized to be a function of a variety of factors. Plants alter the timing and location of foraging dependent on predation risk (Jensen et al. 2011), root herbivory (Stevens and Jones 2006) and competition (Cahill et al. 2010). When measured in terms of movement, we found

Table 1 Results of a linear mixed model testing the effects of the soil resource distribution (heterogeneous or homogeneous), fungal inoculation, and their interactions on total biomass, root to shoot ratios, and the phosphorus and nitrogen shoot concentrations of *Achillea millefolium*

	Biomass			Root: shoot			P content (%)			N content (%)		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Resource distribution	1, 28.2	0.79	0.382	1, 27.8	16.40	<0.001	1, 29.5	0.01	0.928	1, 29.1	26.56	<0.001
Fungal inoculation	1, 26.5	6.55	0.016	1, 26.3	1.87	0.183	1, 28.2	5.67	0.024	1, 27.8	0.005	0.944
Resource distribution × fungal inoculation	1, 26.5	0.92	0.347	1, 26.317	0.061	0.807	1, 28.2	0.005	0.829	1, 27.8	3.97	0.056

that the distribution of soil resources rather than inoculation by soil fungi modified root foraging behaviour.

Root foraging behaviour varied contextually as shifts in root foraging occurred due to resource heterogeneity. Before roots approached pot boundaries, roots growing towards high-quality patches travelled a shorter distance than those grown in homogeneous soils. This finding matches marginal value theorem predictions that organisms should leave low-quality environments earlier than those foraging in high-quality environments (Charnov 1976; McNickle and Cahill 2009). Specifically, roots should venture from a patch only when the resource value has been lowered to its surrounding environment, the time spent in a patch modified by its quality. Consequently, the hierarchy for distance travelled should be heterogeneous soils with high-nutrient patches less than heterogeneous soils with low-nutrient patches less than homogeneous soils, assuming that there are less nutrients in homogeneous soils in the concordant "patch" location. We found however, that the distance travelled by roots did not differ between heterogeneous and homogeneous resource distributions when growth was towards low-quality patches. Thus, the foraging behaviour of roots was affected by the contrast between a nutrient patch and background soil.

Our finding differs from previous work showing that roots travel less in homogeneous soils than in heterogeneous soils (McNickle and Cahill 2009). A notable difference between these experiments is the arrangement of resource patches. Heterogeneous soils in our experiment consisted of high- and low-nutrient patches located on either side of the plant. McNickle and Cahill (2009) arranged both high- and low-nutrient patches on either side of the plant, with their positions switched depending on the treatment. The patch arrangement of McNickle and Cahill (2009) may have resulted in roots responding not only to the patch first encountered, but also to the patch behind. In our experiment, the total biomass of plants was not dependent on soil resource distribution, indicating that there were no size-dependent biases underlying differences in the distance roots travelled. Root foraging behaviours appear to be complicated by nuanced differences in environments, including the spatial arrangement of resource patches.

One of the main corollaries to the marginal value theorem is that the giving-up time decreases more for low- compared to high-quality patches. In addition, shifts in energy expenditure will modify the time an organism forages in a resource patch. We found that neither of these factors modified the time it took roots to move beyond nutrient patches. When in nutrient patches, roots tended to stay longer than those travelling across a similar distance in homogeneous soils, supporting an active foraging response. However, patch quality did not modify how long the roots stayed in nutrient patches. Other studies have found that the presence rather than the quality of patches impacts root growth. For instance, increasing nutrient heterogeneity increased root and shoot biomass of *Abutilon theophrasti*, while patch contrast had no effect on these measures (Lamb et al. 2004).

Under both passive and active foraging models, the distance roots travel from a plant stem should be asymmetric in heterogeneous soils. The directionality of root growth, however, reveals whether plants forage actively or passively. Specifically, if the direction of asymmetry increases towards low-quality patches, this outcome suggests an active foraging response. The opposite would be true for a passive foraging response. We found that asymmetry in bilateral root growth was unrelated to soil resource heterogeneity and fungal inoculation. Though we found empirical support for predictions from the marginal value theorem, we cannot conclude that the foraging behaviour of *A. millefolium* roots is active or passive. Rather, root growth within this species is integrated such that foraging responses are only partly understood by fine-scale nutrient heterogeneity. Fluctuating asymmetry is an important indicator of plant responses to environmental stress (Lempa et al. 2000 and citations therein; Palmer 1996), including parasitism (Cuevas-Reyes et al. 2011). To our knowledge, whether interactions with fungi increase asymmetry in plant root growth has never been examined. Though fungal inoculation decreased biomass of plants, this did not result in increased deviation from symmetry for bilateral root growth. The variation in asymmetry (Fig. S2) is perhaps not surprising given that five- to tenfold variations in lateral root growth rates have been observed for genetically identical plants grown under controlled environments (Forde

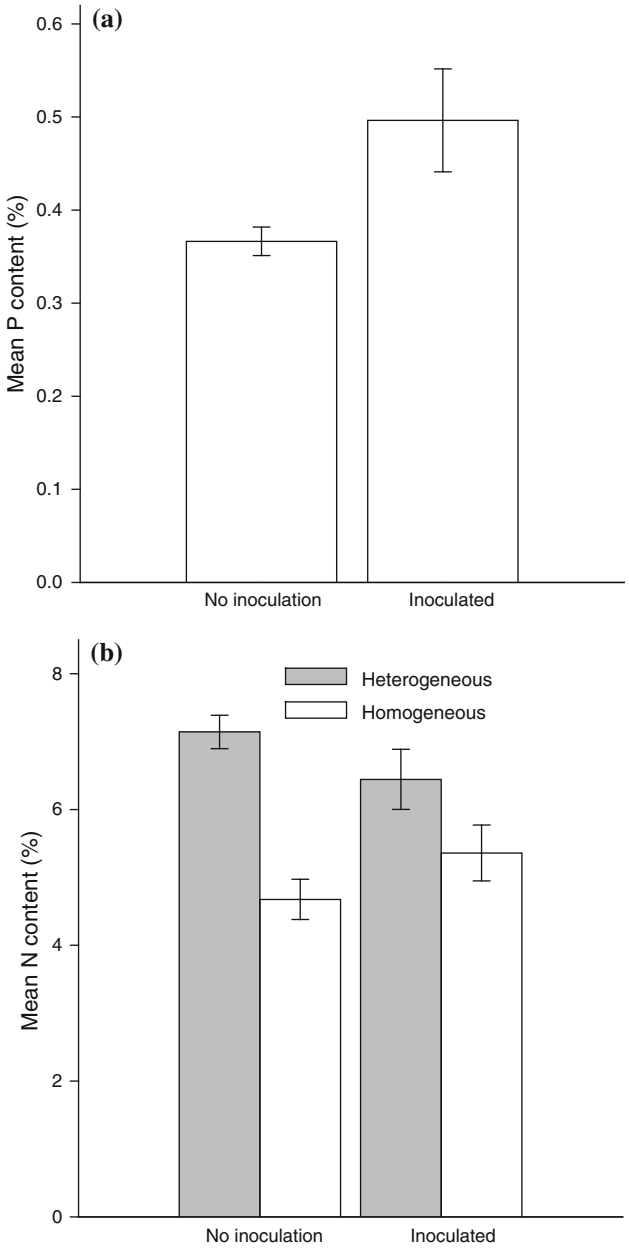

Fig. 4 **a** Shoot phosphorus (%) [$n = 20$ (no inoculation) and $n = 21$ (inoculated)], and **b** shoot nitrogen content (%) ($n = 10$, except for plants growing in inoculated homogeneous soils, for which it was 11) of *Achillea millefolium* in response to fungal inoculation and the soil resource distribution. Untransformed data are presented; analysis was performed on ln-transformed values. All values are mean ± SE

2009). In our experiment, how far roots grew on one side of a plant was positively correlated with how far roots grew on the other. Branches growing in sunny and shaded patches on individual trees of *Pinus sylvestris* also showed correlative growth (Stoll and Schmid 1998), demonstrating that the growth of plant modules is not entirely a function of location conditions.

Though tissue nutrient concentrations changed, plant biomass decreased, indicating that the net benefit of the interaction between soil fungi and plants was negative. The fitness of *A. millefolium* is not well predicted by tissue nutrient concentrations. Allison (2002) found that the total biomass of *A. millefolium* positively affected both seed number and germination success, and tissue nutrient concentration had little effect on these two components of fitness. Increases in P concentration are a hallmark plant response to arbuscular mycorrhizal fungal inoculation (Hodge et al. 2010), but in this case, it could simply be a consequence of the reduced biomass of plants. There was no main effect of fungal inoculation on N concentration; instead, the interaction between soil resource distribution and inoculation determined this plant response. In the absence of inoculation, the spatial configuration of resources determined N concentration. In heterogeneous soils, N concentrations in plants were higher than those grown in homogeneous soils. In part, this may be due to the limited binding sites available for a given soil volume, so that less nutrients are adsorbed by soils when increasing increments of nutrients are added. The presence of fungi may functionally cancel out those differences. Why P, a relatively immobile nutrient, did not show this same pattern is unclear.

Although the plant–fungus interaction was parasitic, fungal inoculation did not cause roots to leave nutrient patches earlier than roots growing in noninoculated soils. To date, the effects of fungal inoculation on root foraging has focussed on identifying changes in the spatial distribution of roots (Cui and Caldwell 1996; Hodge et al. 2000; Wijesinghe et al. 2001), and not necessarily on shifts in foraging behaviour. Our experiment demonstrated that fungal inoculation did not alter the total distance travelled by roots, but it did impact the initial speed at which roots moved through the soil. Roots of inoculated plants approached patch locations slower than those of noninoculated plants, presumably mediated by plant size. Though fungal inoculation reduced the size of the plant, it had no effect on root to shoot ratios. Roots of smaller plants show similar foraging behaviour in heterogeneous resource conditions to those of larger plants.

Acknowledgments We thank Tan Bao, Gordon McNickle, Samson Nyanumba, and Shannon White for critical discussions and readings of the manuscript. Justine D. Karst was supported by an Izaak Walton Killam postdoctoral fellowship, Jonathan A. Bennett by a Natural Sciences and Engineering Research Council of Canada postgraduate scholarship, and James F. Cahill by a Natural Sciences and Engineering Research Council of Canada discovery grant and an accelerator supplemental grant. This experiment was conducted in AB, Canada, and complied with all current provincial and federal laws.

Conflict of interest The authors declare that they have no conflict of interest.

References

Allison VJ (2002) Nutrients, arbuscular mycorrhizas and competition interact to influence seed production and germination success in *Achillea millefolium*. Funct Ecol 16:742–749

Augspurger CK (1983) Seed dispersal of the tropical tree, *Platypodium-elegans*, and the escape of its seedlings from fungal pathogens. J Ecol 71:759–771

Barber I, Huntingford FA (1996) Parasite infection alters schooling behaviour: deviant positioning of helminth-infected minnows in conspecific groups. Proc R Soc Lond B Biol Sci 263:1095–1102

Barber I, Hoare D, Krause J (2000) Effects of parasites on fish behaviour: a review and evolutionary perspective. Rev Fish Biol Fish 10:131–165

Bever JD, Dickie IA, Facelli E, Facelli JM, Klironomos J, Moora M, Rillig MC, Stock WD, Tibbett M, Zobel M (2010) Rooting theories of plant community ecology in microbial interactions. Trends Ecol Evol 25:468–478

Brown JS, Kotler BP (2004) Hazardous duty pay and the foraging cost of predation. Ecol Lett 7:999–1014

Brundrett MC (2009) Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. Plant Soil 320:37–77

Cahill JF, McNickle GG (2011) The behavioural ecology of nutrient foraging by plants. Annu Rev Ecol Evol Systemat 42:289–311

Cahill JF, McNickle GG, Haag JJ, Lamb EG, Nyanumba SM, Clair CCS (2010) Plants integrate information about nutrients and neighbours. Science 328:1657

Cain ML (1994) Consequences of foraging in clonal plant-species. Ecology 75:933–944

Carvalho LM, Correia PM, Ryel RJ, Martins-Loucao MA (2003) Spatial variability of arbuscular mycorrhizal fungal spores in two natural plant communities. Plant Soil 251:227–236

Charnov EL (1976) Optimal foraging, marginal value theorem. Theor Popul Biol 9:129–136

Cuevas-Reyes P, Fernandes GW, Gonzalez-Rodriguez A, Pimenta M (2011) Effects of generalist and specialist parasitic plants (Loranthaceae) on the fluctuating asymmetry patterns of ruprestrian host plants. Basic Appl Ecol 12:449–455

Cui M, Caldwell MM (1996) Facilitation of plant phosphate acquisition by arbuscular mycorrhizas from enriched soil patches. 1. Roots and hyphae exploiting the same soil volume. New Phytol 133:453–460

de Kroon H, Mommer L (2006) Root foraging theory put to the test. Trends Ecol Evol 21:113–116

Farley RA, Fitter AH (1999) Temporal and spatial variation in soil resources in a deciduous woodland. J Ecol 87:688–696

Forde BG (2009) Is it good noise? The role of developmental instability in the shaping of a root system. J Exp Bot 60:3989–4002

Gleeson SK, Fry JE (1997) Root proliferation and marginal patch value. Oikos 79:387–393

Gordon DM (2011) The fusion of behavioural ecology and ecology. Behav Ecol 22:225–230

Grimoldi AA, Kavanova M, Lattanzi FA, Schaufele R, Schnyder H (2006) Arbuscular mycorrhizal colonization on carbon economy in perennial ryegrass: quantification by (CO_2)-C-13/(CO_2)-C-12 steady-state labelling and gas exchange. New Phytol 172:544–553

Hodge A (2004) The plastic plant: root responses to heterogeneous supplies of nutrients. New Phytol 162:9–24

Hodge A, Robinson D, Fitter AH (2000) An arbuscular mycorrhizal inoculum enhances root proliferation in, but not nitrogen capture from, nutrient-rich patches in soil. New Phytol 145:575–584

Hodge A, Helgason T, Fitter AH (2010) Nutritional ecology of arbuscular mycorrhizal fungi. Fungal Ecol 3:267–273

Hoeksema JD, Chaudhary VB, Gehring CA, Johnson NC, Karst J, Koide RT, Pringle A, Zabinski C, Bever JD, Moore JC, Wilson GWT, Klironomos JN, Umbanhowar J (2010) A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. Ecol Lett 13:394–407

Jackson RB, Caldwell MM (1993) The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. Ecology 74:612–614

Jenkins W (1964) A rapid centrifugal-flotation technique for separating nematodes from soil. Plant Disease Report 73:288–300

Jensen EL, Dill LM, Cahill JE (2011) Applying behavioural-ecological theory to plant defence: light-dependent movement in *Mimosa pudica* suggests a trade-off between predation risk and energetic reward. Am Nat 177:377–381

Johnson HA, Biondini ME (2001) Root morphological plasticity and nitrogen uptake of 59 plant species from the Great Plains grasslands, USA. Basic Appl Ecol 2:127–143

Johnson NC, Graham JH, Smith FA (1997) Functioning of mycorrhizal associations along the mutualism-parasitism continuum. New Phytol 135:575–586

Jones MD, Smith SE (2004) Exploring functional definitions of mycorrhizas: are mycorrhizas always mutualisms? Can J Bot 82:1089–1109

Karban R (2008) Plant behaviour and communication. Ecol Lett 11:727–739

Kelly CK (1990) Plant foraging—a marginal value model and coiling response in *Cuscuta-subinclusa*. Ecology 71:1916–1925

Klironomos JN (2003) Variation in plant response to native and exotic arbuscular mycorrhizal fungi. Ecology 84:2292–2301

Klironomos JN, Rillig MC, Allen MF (1999) Designing belowground field experiments with the help of semi-variance and power analyses. Appl Soil Ecol 12:227–238

Lamb EG, Haag JJ, Cahill JF (2004) Patch-background contrast and patch density have limited effects on root proliferation and plant performance in *Abutilon theophrasti*. Funct Ecol 18:836–843

Lefevre T, Lebarbenchon C, Gauthier-Clerc M, Misse D, Poulin R, Thomas F (2009) The ecological significance of manipulative parasites. Trends Ecol Evol 24:41–48

Lempa K, Martel J, Koricheva J, Haukioja E, Ossipov V, Ossipova S, Pihlaja K (2000) Covariation of fluctuating asymmetry, herbivory and chemistry during birch leaf expansion. Oecologia 122:354–360

Levri EP, Lively CM (1996) The effects of size, reproductive condition, and parasitism on foraging behaviour in a freshwater snail, *Potamopyrgus antipodarum*. Anim Behav 51:891–901

McNickle GG, Cahill JF (2009) Plant root growth and the marginal value theorem. Proc Natl Acad Sci USA 106:4747–4751

McNickle GG, St Clair CC, Cahill JF (2009) Focusing the metaphor: plant root foraging behaviour. Trends Ecol Evol 24:419–426

Moore J (1995) The behaviour of parasitized animals. Bioscience 45:89–96

Moore J (2002) Parasites and the behaviour of animals. Oxford University Press, New York

Mummey DL, Rillig MC (2008) Spatial characterization of arbuscular mycorrhizal fungal molecular diversity at the submetre scale in a temperate grassland. FEMS Microbiol Ecol 64:260–270

Packer A, Clay K (2000) Soil pathogens and spatial patterns of seedling mortality in a temperate tree. Nature 404:278–281

Palmer AR (1996) Waltzing with asymmetry. Bioscience 46:518–532

Rajaniemi TK (2007) Root foraging traits and competitive ability in heterogeneous soils. Oecologia 153:145–152

Raveh A, Kotler BP, Abramsky Z, Krasnov BR (2011) Driven to distraction: detecting the hidden costs of flea parasitism through foraging behaviour in gerbils. Ecol Lett 14:47–51

Smilauer P, Smilauerova M (2000) Effect of AM symbiosis exclusion on grassland community composition. Folia Geobot 35:13–25

Smith SE, Read DJ (2008) Mycorrhizal symbiosis, 3rd edn. Academic, London

Stevens GN, Jones RH (2006) Patterns in soil fertility and root herbivory interact to influence fine-root dynamics. Ecology 87:616–624

Stoll P, Schmid B (1998) Plant foraging and dynamic competition between branches of *Pinus sylvestris* in contrasting light environments. J Ecol 86:934–945

Tibbett M (2000) Roots, foraging and the exploitation of soil nutrient patches: the role of mycorrhizal symbiosis. Funct Ecol 14:397–399

Wijesinghe DK, John EA, Beurskens S, Hutchings MJ (2001) Root system size and precision in nutrient foraging: responses to spatial pattern of nutrient supply in six herbaceous species. J Ecol 89:972–983