# Plant root growth and the marginal value theorem

**Gordon G. McNickle[1] and James F. Cahill, Jr.**

Department of Biological Sciences, University of Alberta, CW 405, Biological Sciences Centre, Edmonton, AB, Canada T6G 2E9

All organisms must find and consume resources to live, and the strategies an organism uses when foraging can have significant impacts on their fitness. Models assuming optimality in foraging behavior, and which quantitatively account for the costs, benefits, and biological constraints of foraging, are common in the animal literature. Plant ecologists on the other hand have rarely adopted an explicit framework of optimality with respect to plant root foraging. Here, we show with a simple experiment that the marginal value theorem (MVT), one of the most classic models of animal foraging behavior, can provide novel insights into the root foraging behavior of plants. We also discuss existing data in the literature, which has not usually been linked to MVT to provide further support for the benefits of an optimal foraging framework for plants. As predicted by MVT, plants invest more time and effort into highly enriched patches than they do to low-enriched patches. On the basis of this congruency, and the recent calls for new directions in the plant foraging literature, we suggest plant ecologists should work toward a more explicit treatment of the idea of optimality in studies of plant root foraging. Such an approach is advantageous because it forces a quantitative treatment of the assumptions being made and the constraints on the system. While we believe significant insight can be gained from the use of preexisting models of animal foraging, ultimately plant ecologists will have to develop taxa-specific models that account for the unique biology of plants.

optimal foraging | plant behavior | root foraging | root movement | giving up time

**A**ll life must find and consume resources to sustain itself, and there exists a diverse array of solutions to this basic problem (1–6). Although the proximate mechanisms (sensu 7) of resource collection differ among taxa, they are conceptually linked by a common ultimate cause. Natural selection should favor those individuals who are able to forage more efficiently, within certain lineage-specific biological constraints. One approach that has been used to address issues of foraging behavior has been the application of optimality-based models (8–10). Although natural selection is unlikely to produce perfectly optimal individuals (11, 12), animal behaviorists have been successful at predicting and understanding foraging behavior through the use of an explicitly quantitative treatment of the assumption of optimality. Such an approach is advantageous because it forces the researcher to a priori identify the exact costs and benefits that should be associated with different behaviors. It also forces researchers to quantify their assumptions and the biological constraints on behavior. By using an explicitly quantitative approach one gains a precision in the understanding of the system that cannot be achieved with vague references to "adaptation." This precision can shed light on both the proximate and ultimate causes of behavior and lead to new research directions and improved understanding of behavior regardless of whether the behavior or the organism is strictly optimal (8–10).

Arguably one of the most influential contributions to optimal foraging theory was the marginal value theorem (MVT) (10, 13, 14). MVT uses an optimality framework to predict how organisms should allocate foraging effort to patches of differing quality before leaving, and by extension, predicts broad scale patterns of movement across a landscape. Specifically when foraging activities deplete resource abundance in a patch, MVT predicts: (*i*) the density of resources that remain in a patch when the organism leaves (i.e., the giving-up density) should be equal for all patches regardless of initial patch quality; (*ii*) as the distance between patches increases, the amount of time spent in patches before leaving [i.e., the giving-up time (GUT)] should increase; (*iii*) as average habitat quality increases, GUT should increase; and (*iv*) within a given habitat, the GUT for higher quality patches should be higher than lower quality patches. It is this fourth prediction, concerning GUT within a habitat, that will be the focus of this paper.

Plants exhibit substantial plasticity in growth in relation to environmental heterogeneity, often preferentially placing their foraging organs in areas of high resource concentration (reviewed in refs. 2–4). This phenomenon has been compared to the foraging behavior of animals, and there have been several previous attempts to place plant foraging into the context of MVT (15–18). For example, plants increase root growth (15, 16) and the allocation of parasitic stems (17, 18) into patches of variable quality in a manner consistent with the predictions of MVT. In these studies, and common to most studies of plant foraging, is a focus on biomass distributions, ignoring the potential movement patterns of plant organs, which result in the discovery and eventual exit of patches. This issue of patch leaving behavior is one of the key predictions of MVT, and to our knowledge this issue has not been applied to plants. Here we will focus specifically on plant root foraging behavior, as this area is particularly well studied and most obviously similar to patterns of animal movement.

If we take root growth to be analogous to movement in animals, MVT would predict that actively growing plant roots should not venture outside of a patch until the resource level in that patch had been drawn down to the average resource density in the environment. In other words, those roots that approach the edges of a patch should stop growing until the patch value has been significantly lowered. Thus, the plant could increase its rate of resource capture by focusing all root growth inside the borders of the patch, and only venturing into poorer quality soil once the patch is depleted. If this were true, and occurred locally among all roots within the patch, it would result in broad differences in the overall breadth of the root system of plants growing in heterogeneous soil. Like animals, plants that encounter the most highly enriched patches would travel the shortest distances, compared to plants that encounter patches of lower enrichment. Furthermore, because plants are constructed from semiautonomous metamers, which form the building blocks of their modular bodies (19), we expect this change in distance traveled to be a local response, not a systemic response.
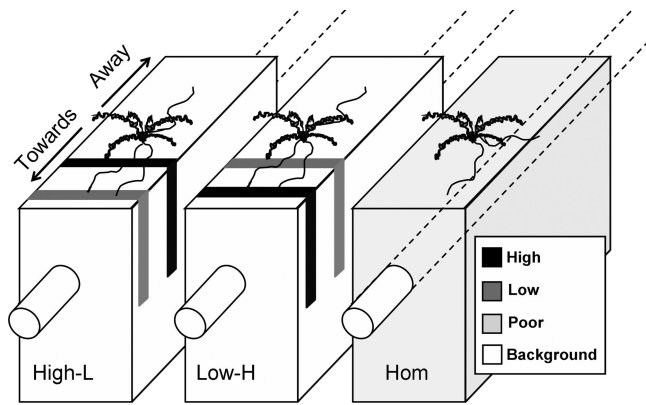
Here we describe an experiment designed to test 2 predictions of MVT concerning patch use behavior: (*i*) plant roots should leave low-enriched patches earlier than highly enriched patches, and (*ii*) plants should allocate more foraging effort to high-quality patches than low-quality patches (15–18), as measured by

**Fig. 1.** Schematic representation of experimental design. Regions of differing soil quality are indicated by regions of darker shading. High-quality soil contained 66% manure mixed with background soil (vol/vol), low contained 25%, poor 4%, and background soil 0%. Transparent plastic tubes spanned the length of each box so that roots traveling away from the shoot could be visualized through the use of a minirhizotron camera inserted into the tubes. Minirhizotron tubes below the soil in the schematic are indicated by dashed lines and are shown for the Hom treatment only. Distance traveled by roots searching for nutrients in the soil was measured as the distance from the base of the shoot to the farthest visible root either toward patches, or away from patches. Schematic is not to scale.

root biomass. We also expect both of these responses to be local rather than systemic because of the modular construction of plants. To test these hypotheses, we grew *Achillea millefolium* plants in soil where they would have access to highly enriched patches, low-enriched patches, or no patches at all (Fig. 1). Patches were placed on 1 side of the shoot only, which allowed us to measure root growth toward and away from patches to distinguish local responses from systemic responses (Fig. 1). We tracked root movement through the use of a minirhizotron camera so that we could measure the total distance traveled either toward patches, or away from patches and thus estimate when plants left patches. Average habitat quality and average distance among patches were held constant and we varied only patch quality and the presence or absence of patches. A critical aspect of our design was that all treatments received the same total amount of nutrient enrichment, but differed only in the pattern of nutrient enrichment (Fig. 1). We conclude the study by resynthesizing some of the existing data in the context of MVT with a goal of assessing the generality of this model for application to plant behavior.

## Results

**Patch Leaving Behavior.** When grown in heterogeneous soil, plant roots grew beyond low-enriched patches earlier than they grew beyond highly enriched patches, resulting in differences in the overall distance traveled by roots among these soil treatments (Fig. 2 *A* and *B*). This finding is indicated by a significant 3-way interaction between body size, direction of growth, and heterogeneity on the total distance traveled by plants over a 36-day period ($F_{2,23} = 5.36$, $P = 0.012$, Fig. 2 *A* and *B*). This complex interaction indicates that plant root growth depends simultaneously on (*i*) whether the plant is grown in heterogeneous or homogeneous soil—roots travel less in homogeneously poor soil, (*ii*) whether the roots encounter a patch or not—they travel farther when they encounter a patch (i.e., this is a local response and not a systemic response), and (*iii*) the size of the plant—bigger plants have more roots and therefore travel farther than smaller plants. The most important conclusion of this result is that, as predicted by MVT, plant roots stay longer in more highly
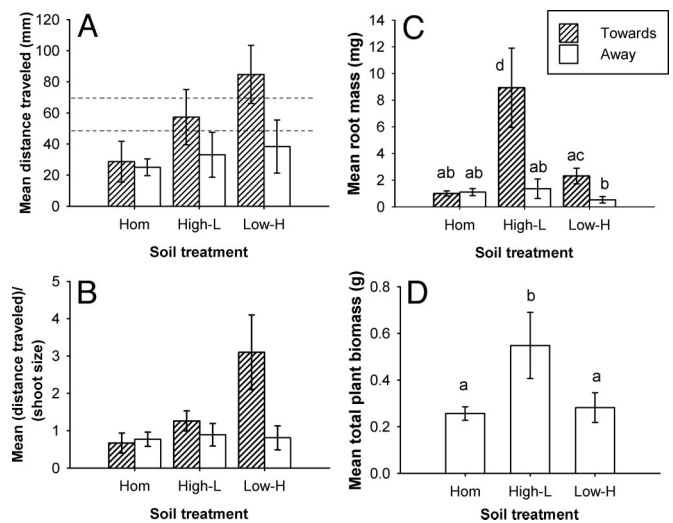


**Fig. 2.** Summary of the optimal patch use behavior of plants according to the hypotheses generated by marginal value thereom. (*A*) Mean raw distance traveled by plant roots through the soil across all treatments without accounting for shoot size, after 36 days of growth. The location of the first patch is denoted by dashed horizontal lines. (*B*) Mean distance traveled by roots standardized by plant size, all treatments after 36 days of growth. This accounts for differences in distance traveled by roots that are related only to plant size. (*C*) Mean soil exploration measured as biomass of roots inside the boundaries of the first patch only (toward) and the equivalent location on the opposite side of the plant (away) for each treatment. Letters above bars represent the differences in mean proliferation designated by the least square means post hoc comparison in SAS. Data are after 48 days of growth. (*D*) Mean total biomass of plants grown in each soil treatment after 48 days of growth. Changes in biomass reflect differences in nutrient uptake among plants. We did not directly measure plant fitness. Letters above the means indicate statistical differences detected by a Tukey's test. Error bars in all panels are 1 SE.

enriched patches than in low-enriched patches before moving (Fig. 2 *A* and *B*).

**Foraging Effort Within Patches.** Plants allocated more foraging effort per unit soil volume (root biomass) to highly enriched patches than to low-enriched patches (Fig. 2*C*). The amount of foraging effort was the same in homogeneous soil as it was in the background soil in the heterogeneous soil treatment (Fig. 2*C*). This is evidenced as a 2-way interaction between soil heterogeneity and the direction of growth on total foraging effort ($F_{2,26} = 5.78$, $P = 0.008$, Fig. 2*C*), indicating that the amount of root growth in a particular soil location depends upon the quality of the soil at that location. Plants allocate more root growth in areas of better quality soil. Because plant root allocation differed as a function of the side of the plant in which roots were measured (side with the patch vs. side without the patch), we can infer that plant root responses are local and not systemic (Fig. 2*C*).

**Short-Term Benefits.** Total plant biomass was larger ($F_{2,24} = 5.31$, $P = 0.012$) when plants encountered high-quality patches than in the other treatments (Fig. 2*D*). Because a separate experiment (see *Methods*) showed that our background soil limited plant growth, this result suggests that the foraging efforts of plants in high-quality patches lead to increased nutrient capture in the short term. There was no difference between the low-enriched patches and homogeneous soil for total plant growth (Fig. 2*D*). Biomass in this context only reflects differences in short-term nutrient capture and may or may not correlate to long-term fitness.

## Discussion

The results from our experiment are consistent with both of the hypotheses generated by MVT, with plants spending both more

     McNickle and Cahill

time (Fig. 2 *A* and *B*) and effort (Fig. 2*C*) in highly enriched patches than in low-enriched patches. This study creates a picture of plant root movement, in relation to patches, that mirrors patterns of movement among patches in animals. Both plants and animals that encounter high-quality patches will remain in those patches longer (10, 14), and as a result, travel shorter distances in search of resources compared to conspecifics that encounter low-quality patches (Fig. 2 *A* and *B*). To our knowledge this is the first time that plant root movement patterns have been linked to the idea of patch leaving as envisioned by the MVT. However, this is not the first study to link patterns of biomass allocation in relation to resource heterogeneity to MVT (15–18).

**Links to the Marginal Value Thereom.** One of the predictions of MVT is that organisms should invest foraging effort in proportion to patch quality. This has been demonstrated for the allocation of foraging effort of roots (15, 16) and parasitic stems (17, 18), which occur in proportion to patch quality as predicted by MVT. Patterns of fine root biomass allocation in response to soil nutrient heterogeneity are well studied and there are studies in the literature that have similarly documented this relationship between patch quality and foraging effort, even if the original authors did not cast them in the context of MVT. Not all studies of root foraging measure patches of different quality, but when they do, almost every species studied expends foraging effort in proportion to patch quality (e.g., 20–24). In other words, plants that focus root growth primarily in nutrient-rich soil, presumably maximize the benefits of foraging and minimize the costs of root growth and nutrient uptake.

Another prediction of MVT is that organisms should spend less effort in patches as total habitat quality increases. Less data are available to test this prediction, although available data suggest this hypothesis may be supported. Lamb et al. (20) found fewer roots were produced by plants as total habitat quality increased and when the total number of patches remained constant. However, there was only a nonsignificant trend toward reduced effort in patches as habitat quality increased (20). Similar results have been found for competing plants that avoid areas of high competition in favor of root-free soil, where resource uptake is presumably higher (16). In general, plants seem to favor soil with low competition over soil with large numbers of competitors (25). Few studies have included experimental designs that test this specific hypothesis of MVT; however, this preliminary evidence suggests that roots behave in a way that is predicted by MVT.

A third prediction of MVT is that the density of resources that remain in a patch when the organism leaves (the "giving-up density") should be equal among all patches regardless of initial quality (13). This hypothesis remains untested for plant root growth.

**Similarity to Daughter Ramet Placement.** Similar to the foraging response of fine roots, the vegetative spread of clonal plants through the environment tends to track heterogeneity in resource distribution and has also been described as foraging (26–28). Generally, clonal plants increase the density of daughter ramets inside high-quality patches compared to the background environment, which increases the level of resource capture (26–28). This allocation of ramet biomass in relation to heterogeneity also matches the predictions of MVT, although again most authors do not link their results to an optimality framework. Clonal plants also decrease the spacer length between daughter ramets in high-quality patches compared to other areas of the environment (26–28). This change in spacer length is traditionally thought to serve only as a mechanism for increasing foraging effort (26–28). However, the reduction of spacer length in high-quality patches means that plants will

spend more time in those patches compared to background soil. This behavior in stem plasticity is similar to the behavior of the fine roots of *A. millefolium* described in this study (Fig. 2 *A* and *B*) despite the vast physiological differences between stems and roots. This suggests that there is likely a similar underlying ultimate cause behind these behaviors. Specifically, those plant species that were capable of devoting more time and effort to highly enriched soil, gathered more resources, had higher fitness, and left more descendants than those who were incapable of this behavior.

**Using Optimality Theory to Move Forward.** Although most species respond to nutrient patches through precise placement of biomass into patches, there are some that do not (3, 4). We suggest that an optimality framework may provide clues to the range of responses among species and among contexts. Optimal foraging does not mean that an organism must always respond to a resource stimulus as has been expected in many plant studies. Instead the idea of optimality means that organisms should maximize benefits and minimize costs subject to certain constraints (8–10). When the potential costs exceed the benefits the organism should not respond to the resource. By taking a comparative approach to measuring costs and benefits of foraging and quantifying ones assumptions and the biological constraints, those species with low foraging ability may turn out to be the most important for assessing the applicability of an optimality framework.

Despite the fact that few authors have linked their results to MVT, the data from this study and others suggest much of the patch use behavior of plants is at least qualitatively consistent with a framework of optimality described by MVT. On the basis of this congruency, we suggest that plant ecologists should begin to develop more explicitly quantitative frameworks of optimal foraging in plants. As we have seen, MVT can make surprisingly good qualitative predictions about plants, despite the fact that it was developed with animal foraging in mind. However, the development of plant-specific models of optimal foraging will likely lead to more precise predictions about plant behavior and ultimately a better understanding of plant foraging. These models should take into account the issues such as modular growth, which is one of the biggest differences between plants and (most) animals (19). But why does this matter and how does the synthesis above differ from a series of nice stories about adaptation?

Plant ecologists have admittedly gone down some blind alleys in the study of plant foraging (29). For example, the study of root foraging for several decades has often focused on possible tradeoff in the scale and precision of root foraging (29–33). The idea behind the scale–precision tradeoff was that species with large-scale root systems would be imprecise foragers, and species with small-scale root systems should be precise foragers (30, 31). In other words, this theory implicitly assumed that the ultimate evolutionary drivers of behavior should be reversed depending on the size of the plant, or at least that the proximate abilities of closely related species differed as a function of their size. After decades of research on hundreds of species, 2 recent metaanalyses of this literature do not result in support for a tradeoff in scale and precision (32, 33). With the doubt cast on this dominant paradigm, plant ecologists are in need of new directions for foraging theory (29, 32, 33 but see ref. 31).

Given the incredible success of an optimality framework for the interpretation of animal foraging (9, 10), and the fact that much of the relevant plant foraging behavior described above is consistent with an optimality framework, we suggest that plant ecologists should work toward an explicitly quantitative development of optimal foraging theory for plants. This will involve a change of focus in this research program to measuring potential fitness losses through missed opportunities, the potential benefits of resource

**ECOLOGY**

capture for fitness gain, and how these benefits and costs interact to shape the total response of foraging plants. It will also require plant ecologists to quantify their assumptions and the constraints on behavior. Such an explicitly quantitative approach takes the vague notion of a behavior being "adaptive" which has always been assumed and brings it into sharper focus by precisely quantifying what is meant by the word adaptive. This shift in thinking about plant behavior can be simplified by gaining insight from the lessons learned throughout the history of the animal foraging literature (reviewed in refs. 10, 14) as we have shown with a combination of experiment and literature review.

## Conclusions

Our data and much of the existing data in the literature show that patterns of plant root growth through soil qualitatively mirror optimal movement strategies of animals, as predicted by a model of optimal foraging, the marginal value theorem. Our predictions were born out of a theory of animal movement, but they are consistent with much of the empirical evidence concerning plant responses to soil patches. We have argued that a more explicit treatment of the concept of optimality will bring a level of quantitative precision to the study of plant behavior that is sorely needed. We have discussed one such model of optimality from the animal literature and shown how it can provide novel insights into plant ecology. However, ultimately we believe that plant ecologists will need to forge their own optimality theories that account for the unique biology of plants.

## Methods

**Study Species.** *A. millefolium* is a herbaceous perennial species that is native to much of the northern hemisphere and is thought to have a naturally circumpolar distribution (34). Seed was obtained from a local native seed distributor (Bedrock Seedbank) who obtains and propagates seed from local populations. We selected *A. millefolium* as the study species for this experiment because the foraging response of *A. millefolium* is well documented, with evidence that it does exhibit a high degree of foraging precision (35–37). Not all plant species respond to heterogeneity and it was important for this study that we focus on a plant that was known to exhibit a strong foraging response.

**Experimental Setup.** *A. millefolium* plants were grown in three soil environments, each of which contained the same total amount of nutrients, but varied in the distribution of those nutrients (Fig. 1). The three soil treatments were (*i*) High-L, background soil with a highly enriched patch near 1 side of the plant (66% vol/vol steer manure, Nu-Grow IP); (*ii*) Low-H, background soil with a low-enriched patch near 1 side of the plant (25% steer manure); and (*iii*) Hom, a spatially uniform soil environment (4% steer manure spread evenly throughout the soil). The background soil used in the 2 heterogeneous treatments consisted of a 3:1 ratio of washed sand to commercial top soil, and it was this soil that was amended with manure to create nutrient enrichment. We used *A. millefolium* plants in a separate experiment to bioassay each of our soil quality designations (described below).

Individual plants grew in the center of $30 \times 12 \times 30$-cm wooden boxes (Fig. 1), with 10 replicate boxes per treatment. Patches, when present, were 2 cm wide and spanned the width of the pot. Patches were placed 6 cm away from the plant on only 1 side of the stem, which allowed us to differentiate between a localized response (only roots on the side with the patch would vary among treatments) and a systemic response (roots of both sides would respond). Heterogeneous soil treatments received a second patch of opposite quality to the first, which was placed 12 cm from stems on the same side of the pot as the first patch (Fig. 1). This was done to ensure that each pot received the same total amount of nutrients. However, the experiment was stopped before plants reached the second set of patches. Plants were grown in a growth chamber in the University of Alberta, Department of Biological Sciences Biotron facility, with a 16:8 light:dark cycle. Plants were watered daily with an automatic mist sprinkler system, preventing any appearance of water stress.

Before the experiment, a clear plastic minirhiztron tube was inserted lengthwise through each box 5 cm below the surface of the soil (Fig. 1). This tube allowed us to nondestructively measure the growth rate of roots through visual observation with a minirhizotron camera (Bartz Technology). It was not possible to measure the exact giving-up time (GUT) for our plants because fine-scale movements of roots turned out to be too difficult to measure as roots would

often move in and out of the field of view. Instead, we measured the total distance traveled by plant roots as a proxy for GUT. Distance traveled was measured as the distance from the base of the shoot to the farthest visible root either toward patches or away from patches (Fig. 1). Patch and shoot locations were marked on the rhizotron tube before the start of the experiment and patch soil was visually distinguishable from background soil. Root images were captured every 6 days to monitor root progress through the soil volume. Root tracing was performed with Win RhizoTron v2007b (Regent Instruments).

Because small plants have few roots relative to large plants, we expected size-dependent responses to the soil treatments. To estimate plant size, we measured the length of the longest leaf on each plant every 6 days, which we knew from experience was a correlate of total plant biomass in *A. millefolium*. To confirm the correlation between leaf length and total biomass, we performed a linear regression on leaf length from the day of plant harvest to the total dry weight of plants from our main experiment. Leaf and biomass data were log transformed and analyzed using linear regression in SAS v 9.1 (SAS Institute). There were no differences among treatments, the regression was highly significant ($F_{1,26} = 209$, $P < 0.0001$) and leaf length explained 89% of the variation in total plant biomass. This indicates that length of longest leaf was a good predictor of total dry weight.

To determine potential short-term biomass effects of the treatments, plants were harvested when the mean foraging distance of roots from at least 1 treatment approached the second patch (day 48). This was done to allow growth benefits from root foraging activities in the first patch to accrue without allowing potential confounding effects associated with accessing the second patch. Shoots were cut at the soil surface and dried at 60 °C until they reached a constant mass. Two $2.5 \times 5$-cm root cores were taken from the "toward" side of the pot inside the first patch (or equivalent location in treatment Hom) and pooled, and 2 root cores were taken from the same location on the "away" side of the plant. Roots were stored at $-20$ °C and washed in a 1-mm sieve, dried at 60 °C, and weighed.

**Statistical Analyses.** We noticed that the maximum distance traveled by roots began to vary among soil treatments after 18 days, and the general pattern of growth rate among treatments was similar from that point on. Thus data from after 36 days only, were analyzed using the PROC GLIMMIX procedure for generalized linear mixed models (GLMMs) in SAS (v 9.1, SAS Institute). The model included direction of growth (toward, away) and soil treatment (High-L, Low-H, Hom) as main effects, length of longest leaf (leaf size) as a covariate, and box as a random factor nested in soil treatment to control for pseudoreplication. The data were fit to a negative binomial distribution, with a convergence criteria of $1 \times 10^{-6}$ (pconv = 1EXP-6). The fit of the model was 1.00 (generalized $\chi^2$/df).

Root mass data were analyzed using the PROC GLIMMIX procedure for GLMMs in SAS. The model included direction of growth (toward, away) and soil treatment (High-L, Low-H, Hom) as main effects and box as a random factor nested in soil treatment to control for pseudoreplication. The data were fit to a negative binomial distribution, with a convergence criteria of $1 \times 10^{-6}$ (pconv = 1EXP-6). The fit of the model was 0.77 (generalized $\chi^2$/df). Means were compared using the nlsmeans post hoc analysis in SAS.

Total plant biomass data were log transformed for normality and analyzed using the PROC ANOVA procedure in SAS with soil treatment as the main factor. Means were compared using a post hoc Tukey's test in SAS.

**Soil Bioassay.** In a separate experiment we performed a bioassay of soil quality using *A. millefollium* plants on pure batches of our 4 different soil types to validate our assertion that high-quality soil > low > poor = background soil for plant growth. We did not expect that poor-quality soil would differ from background soil. Plants were grown in 15-cm diameter cylindrical pots on pure high (66% vol/vol steer manure), low (25% vol/vol steer manure), poor (4% vol/vol steer manure), and background soil (0% vol/vol steer manure). After 6 weeks, the experiment was harvested. Shoots were collected and dried at 60 °C and weighed. Shoot mass was log transformed for normality and analyzed using the PROC ANOVA procedure in SAS with soil type as the main factor. Means were compared using a post hoc Tukey's test in SAS. Plant biomass was largest in high-quality soil, intermediate in low-quality soil, and plant size in homogeneous and background soil were smallest but did not differ from each other ($F_{3,29} = 20.16$, $P < 0.0001$). This shows that our ranking and designation of soil quality (i.e., high > low > background = Hom) for *A. millefolium* growth was correct.

1. Krebs JR, Erichsen JT, Webber MI, Charnov EL (1977) Optimal prey selection in Great Tit (*Parus major*). *Anim Behav* 25:30–38.
2. Karban R (2008) Plant behaviour and communication. *Ecol Lett* 11:727–739.
3. Hutchings MJ, de Kroon H (1994) Foraging in plants: The role of morphological plasticity in resource acquisition. *Adv Ecol Res* 25:159–238.
4. Hodge A (2004) The plastic plant: Root responses to heterogeneous supplies of nutrients. *New Phytol* 162:9–24.
5. Heineman RH, Springman R, Bull JJ (2008) Optimal foraging by bacteriophages through host avoidance. *Am Nat* 171:E149–E157.
6. Charnov EL (1976) Optimal foraging: Attack strategy of a mantid. *Am Nat* 110:141–151.
7. Tinbergen N (1963) On aims and methods in ethology. *Z Tierpsychol* 20:410–433.
8. Smith JM (1978) Optimization theory in evolution. *Annu Rev Ecol Syst* 9:31–56.
9. Stearns SC, Schmidhempel P (1987) Evolutionary insights should not be wasted. *Oikos* 49:118–125.
10. Stephens DW, Brown JS, Ydenberg RC eds (2007) *Foraging: Behavior and Ecology* (Univ of Chicago Press, Chicago).
11. Gould SJ, Lewontin RC (1979) Spandrels of San-Marco and the Panglossian paradigm: A critique of the adaptationist program. *Proc R Soc Lond Ser B Biol Sci* 205:581–598.
12. Pierce GJ, Ollason JG (1987) Eight reasons why optimal foraging theory is a complete waste of time. *Oikos* 49:111–118.
13. Charnov EL (1976) Optimal foraging, marginal value theorem. *Theor Popul Biol* 9:129–136.
14. Stephens DW, Krebs JR (1986) *Foraging Theory* (Princeton Univ Press, Princeton).
15. Gleeson SK, Fry JE (1997) Root proliferation and marginal patch value. *Oikos* 79:387–393.
16. Gersani M, Abramsky Z, Falik O (1998) Density-dependent habitat selection in plants. *Evol Ecol* 12:223–234.
17. Kelly CK (1990) Plant foraging: A marginal value model and coiling response in *Cuscuta subinclusa. Ecology* 71:1916–1925.
18. Kelly CK (1992) Resource choice in *Cuscuta europaea. Proc Natl Acad Sci USA* 89:12194–12197.
19. de Kroon H, Huber H, Stuefer JF, van Groenendael JM (2005) A modular concept of phenotypic plasticity in plants. *New Phytol* 166:73–82.
20. 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.
21. Pregitzer KS, Hendrick RL, Fogel R (1993) The demography of fine roots in response to patches of water and nitrogen. *New Phytol* 125:575–580.
22. Jackson RB, Caldwell MM (1989) The timing and degree of root proliferation in fertile-soil microsites for 3 cold-desert perennials. *Oecologia* 81:149–153.
23. Drew MC (1975) Comparison of effects of a localized supply of phosphate, nitrate, ammonium and potassium on growth of seminal root system, and shoot, in barley. *New Phytol* 75:479–490.
24. Fransen B, de Kroon H (2001) Long-term disadvantages of selective root placement: Root proliferation and shoot biomass of two perennial grass species in a 2-year experiment. *J Ecol* 89:711–722.
25. Schenk HJ, Callaway RM, Mahall BE (1999) Spatial root segregation: Are plants territorial? *Adv Ecol Res* 28:145–180.
26. Dekroon H, Hutchings MJ (1995) Morphological plasticity in clonal plants: The foraging concept reconsidered. *J Ecol* 83:143–152.
27. Birch CPD, Hutchings MJ (1994) Exploitation of patchily distributed soil resources by the clonal herb *Glechoma hederacea. J Ecol* 82:653–664.
28. Wijesinghe DK, Hutchings MJ (1999) The effects of environmental heterogeneity on the performance of *Glechoma hederacea*: The interactions between patch contrast and patch scale. *J Ecol* 87:860–872.
29. de Kroon H, Mommer L (2006) Root foraging theory put to the test. *Trends Ecol Evol* 21:113–116.
30. Campbell BD, Grime JP, Mackey JML (1991) A trade-off between scale and precision in resource foraging. *Oecologia* 87:532–538.
31. Grime JP (2007) The scale-precision trade-off in spacial resource foraging by plants: Restoring perspective. *Ann Bot* 99:1017–1021.
32. Kembel SW, de Kroon H, Cahill JF, Mommer L (2008) Improving the scale and precision of hypotheses to explain root foraging ability. *Ann Bot* 101:1295–1301.
33. Kembel SW, Cahill JF (2005) Plant phenotypic plasticity belowground: A phylogenetic perspective on root foraging trade-offs. *Am Nat* 166:216–230.
34. Purdy BG, Bayer RJ (1996) Genetic variation in populations of the endemic *Achillea millefolium ssp megacephala* from the Athabasca sand dunes and the widespread *ssp lanulosa* in western North America. *Can J Bot* 74:1138–1146.
35. 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.
36. Rajaniemi TK (2007) Root foraging traits and competitive ability in heterogeneous soils. *Oecologia* 153:145–152.
37. Rajaniemi TK, Reynolds HL (2004) Root foraging for patchy resources in eight herbaceous plant species. *Oecologia* 141:519–525.

ECOLOGY