



Root foraging theory put to the test

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Roots have a tremendous plasticity that has long fascinated plant scientists. Root proliferation into enriched soil patches is commonly considered as a way for plants to acquire patchily distributed soil resources. In a recent synthetic study involving the responses of over 100 species, Kembel and Cahill concluded that long-standing generalizations explaining variation in root proliferation should be reconsidered.

Root proliferation and foraging precision

Systematic experimental research into root proliferation began during the 1970s, with experiments by Drew and co-workers with barley *Hordeum vulgare* [1]. Their results demonstrated that plants whose main roots were only partly supplied with nutrients grew as fast as plants that were under homogeneously distributed high nutrient conditions. Using root maps (Box 1), Drew *et al.* argued that this root growth was due to prolific lateral root formation in the nutrient-rich zone and the higher growth rate of these lateral roots. Many experiments on root responses to heterogeneously distributed nutrients in the soil have since followed. In a new paper, Kembel and Cahill [2] present the state-of-the-art of our current knowledge by reanalysing data from two large comparative studies [3,4] and from a third data set comprising the results of a large number of other root-foraging studies.

An important parameter in studies of root proliferation is the degree of selective root placement (or 'root foraging precision'), defined as the proportion of the root biomass (or root surface area) of a plant located in high-nutrient hotspots rather than in low-nutrient background soil. Kembel and Cahill found this parameter to be phylogenetically and taxonomically conserved. Their meta-analyses [2] showed that dicots were generally more responsive than were monocots, but the differences were small. However, there was significant variation in selective root placement among species. Some species placed most of their roots in the nutrient-rich patches whereas the roots of other species showed no selectivity and equally distributed their roots over rich and poor parts of the soil.

Explaining root proliferation

Current explanations for variation in root proliferation among species can be traced back to Grime's plant strategy theory [5,6]. One hypothesis is that species with high relative growth rates (RGR) from relatively

productive nutrient-rich environments rely more on morphological plasticity than do species with low RGRs from relatively infertile environments [5]. Grime later introduced the idea of dominant and subordinate species within communities [6]. He proposed that dominants are characterized by rapid growth and large size, by which they monopolize the available above- and belowground resources, but in a rather coarse-grained way ('high-scale foraging') [7]. Subordinates can coexist by the precise placement of their leaves and roots into high-resources patches that remain unexplored by the dominants ('high precision foraging'). Campbell *et al.* [7] thus suggested 'a scale-precision tradeoff' of foraging, which has received much attention, particularly in studies of root plasticity (e.g. [8–12]).

Theory put to the test

Using their large data sets, Kembel and Cahill [2] tested both the RGR and the scale-precision tradeoff hypotheses, finding support, albeit in only one of the three data sets, for a weak positive relationship between foraging precision and RGR. Earlier support for this hypothesis was equally mixed, with either a positive or no correlation found between foraging precision and growth rate [10].

Testing the scale-precision tradeoff was problematic because 'scale', originally defined as 'the total dry weight of the root mass increment by the plant in undepleted [i.e. enriched] sectors of the rooting volume' [7], is unsuitable for comparisons in which patch size and study duration differ. As a substitute (and independent) measure of scale, Kembel and Cahill chose plant height at maturity and found significantly positive correlations between the different measures of scale for the data sets that could be tested.

Studies prior to that by Kembel and Cahill [2] with smaller numbers of species (6–10) also found significant correlations between measures of scale and precision: one study found the correlation to be significantly negative [9], whereas, in three other studies, the correlation was significantly positive [8,10,11]. Although a reanalysis of the eight species on which the scale-precision tradeoff hypothesis was originally based [7] confirmed the significant negative correlation between scale and precision, the two community-wide comparisons (USA Great Plains flora [4], 59 spp, and British flora [3], 43 spp) rendered non-significant correlation coefficients, irrespective of the measure of scale used (J.C. Cahill, personal communication). A similar result was obtained for the third data set. Although evidence so far for the scale-precision tradeoff was mixed at best, Kembel and Cahill found no

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Box 1. Root proliferation in nutrient hotspots in the soil

In an example of a root proliferation study, Drew and Saker [1] grew barley plants *Hordeum vulgare* in small containers divided into three horizontal compartments and filled with sand. The middle compartment received a full nutrient solution, whereas the top and bottom segments were exposed to nutrient solution without phosphate. The authors found profuse development of the first- and second-order lateral roots, but only on the segment of the seminal root in the middle compartment (Figure 1; scale bar = 10 cm; reproduced, with permission,

from [1]). This localized root development into nutrient hotspots is referred to as either root proliferation or selective root placement.

Plants that were supplied with phosphate over only 4 cm of their seminal root length in the middle segment achieved growth rates that were similar to plants that received phosphate over their entire root system. Similar experiments with nitrogen resources revealed similar results [1]. For reasons of clarity, Figure 1 shows only one out of several primary roots of the entire root system.

support in the large data sets, despite the statistical power of their analyses [2].

Concepts of scale and precision reconsidered

The results of Kembell and Cahill [2] call for a reconsideration of scale and precision as general measures of foraging ability in plants. Foraging precision is not a fixed species trait but one that can vary considerably with, for example, plant developmental stage [12]. Some of the inconsistencies among the previous comparative studies [7–11] can thus be explained by differences in growing conditions, experimental design, the developmental stage of the experimental plants [12] and possibly phylogenetic effects [2]. Species differences in developmental rate can also blur community-wide comparisons based on tests with plants of fixed developmental stage under a limited set of conditions. Any measure of foraging scale as a fixed species trait is equally problematic, because it attempts to quantify plant size, again a measure that is extremely variable. Finally, the original measure of scale has a more fundamental problem in the scale-precision context because defining scale in terms of (part of the) root biomass confounds the axes of scale and precision. With root biomass in enriched patches as a common parameter in both scale and precision, it is likely that some of the scale-precision correlations observed are spurious.

Despite these conceptual problems, evidence is accumulating that root biomass (i.e. scale), selective root placement (i.e. precision) and the growth rate of plants all contribute to more effective foraging in a competitive setting. To compete successfully for finite patches of nutrients, a rapid exploitation of the patches is necessary. Root proliferation in nutrient hotspots might lead to resource pre-emption [13] and convey competitive ability underground [14]. Moreover, faster growing species will be more effective foragers because their higher growth rates enable them to ‘discover’ and exploit nutrient patches faster [15]. The positive correlations among scale, precision and RGR found in some of the data sets [2] are suggestive of functional relationships and require further study. The observations of Kembell and Cahill [2] are thus consistent with Grime’s original hypothesis on growth rate and root plasticity [5].

Prospects of root foraging studies

The results of Kembell and Cahill [2] leave much of the variation in root proliferation among species unexplained.

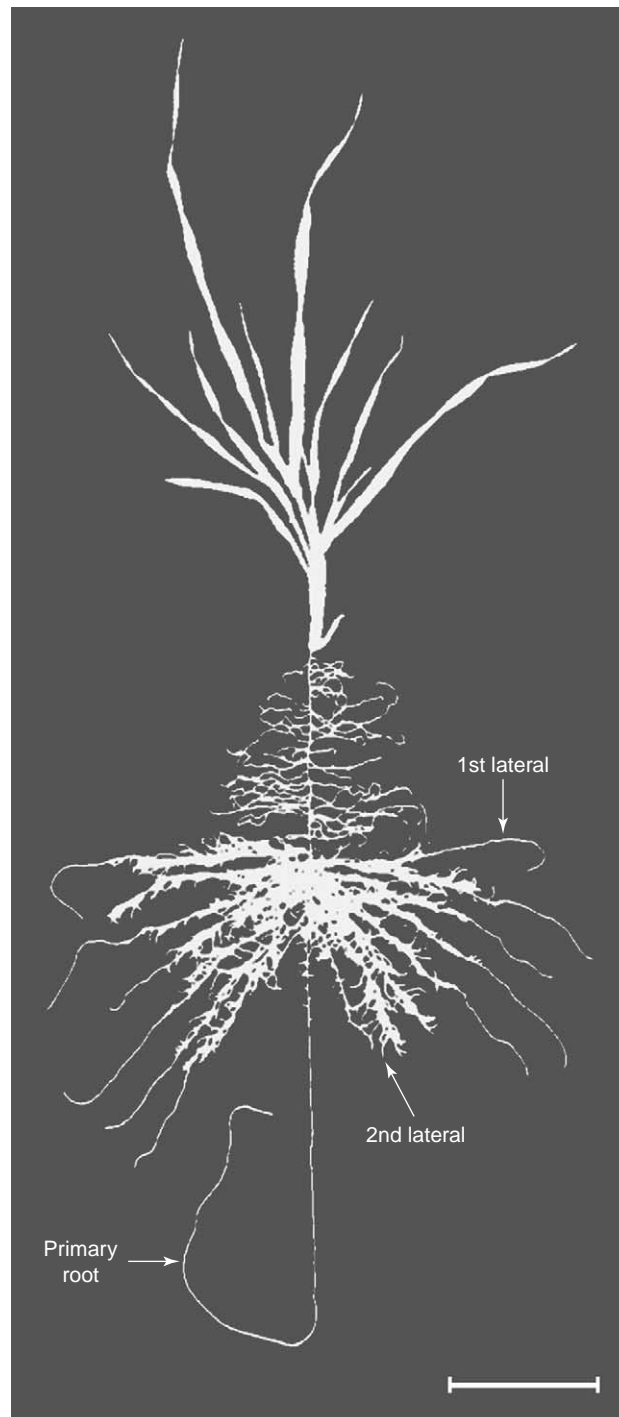


Figure 1.

Grime's original plant strategy concept is a source of inspiration with which to tackle this unsolved issue, as he stressed that the costs and benefits of plasticity are decisive for the selection of plasticity [5]. However, the costs and benefits of root plasticity have not yet received the attention that they deserve. This is particularly surprising given that they also have a key role in studies of plasticity in general [16], from which studies on root proliferation have perhaps been conceptually too isolated. The use of methodologies such as (evolutionary) cost-benefit analyses and the examination of trait correlations [17] could lead to surprising insights in root studies. For example, root proliferation in nutrient hotspots might correlate mechanistically with other root characteristics, such as responses to soil moisture [18]. It might be that these other traits, rather than root proliferation itself, render fitness benefits to the plant. If so, it is theoretically possible that the root proliferation that we observe is a non-adaptive by-product of a trait that remains unstudied.

Root-foraging studies have also developed independently from studies of the soil processes that determine belowground spatial and temporal heterogeneity. Many authors have linked root responses to patterns of solute movement in the soil, bearing mostly on agronomic research. However, in natural soils, it is biogeochemical and rhizosphere processes that generate the fluxes and patterns of nutrient release belowground. Recent progress in these fields reveals a wealth of relevant information [19] that should be integrated with studies of root foraging. For example, we are beginning to further understand how the dynamics of nitrogen hotspots emerge as a result of fine-grained shifts in mineralisation and immobilisation, influenced by the roots both directly and indirectly through mycorrhiza and manipulation of soil microbes [19]. These developments call for a multidisciplinary approach to studies of root plasticity, combining expertise from plant ecology, evolutionary biology and biogeochemistry. Only in this way will the fascinating phenomenon of root foraging reveal its true nature.

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