Improving the Scale and Precision of Hypotheses to Explain Root Foraging Ability

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Background Numerous hypotheses have been proposed to explain the wide variation in the ability of plants to forage for resources by proliferating roots in soil nutrient patches. Comparative analyses have found little evidence to support many of these hypotheses, raising the question of what role resource-foraging ability plays in determining plant fitness and community structure.

Scope In the present viewpoint, we respond to Grime’s (2007; Annals of Botany 99: 1017–1021) suggestion that we misinterpreted the scope of the scale–precision trade-off hypothesis, which states that there is a trade-off between the spatial scale over which plant species forage and the precision with which they are able to proliferate roots in resource patches. We use a meta-analysis of published foraging scale–precision correlations to demonstrate that there is no empirical support for the scale–precision trade-off hypothesis. Based on correlations between foraging precision and various plant morphological and ecophysiological traits, we found that foraging precision forms part of the ‘fast’ suite of plant traits related to rapid growth rates and resource uptake rates.

Conclusions We suggest there is a need not only to examine correlations between foraging precision and other plant traits, but to expand our notion of what traits might be important in determining the resource-foraging ability of plants. By placing foraging ability in the broader context of plant traits and resource economy strategies, it will be possible to develop a new and empirically supported framework to understand how plasticity in resource uptake and allocation affect plant fitness and community structure.

Key words: Root foraging, phenotypic plasticity, scale, precision, resource uptake strategies, traits.

INTRODUCTION

The proliferation of roots in nutrient-rich patches is a fascinating, and well-studied, example of morphological plasticity by plants. Why do plants bother to proliferate roots into nutrient patches (Robinson, 1996), and what are the consequences of differences in root proliferation ability for plant fitness, community structure and nutrient dynamics? Plant species vary greatly in their ability to proliferate roots in response to nutrient heterogeneity (Kembel and Cahill, 2005), and many researchers have sought explanations for the differential ability of plants to proliferate roots. Hypotheses have been adaptive (proliferation increases nutrient uptake during competition; Hodge \textit{et al.}, 1999), trade-off-based (proliferation increases the fitness of subdominant species; Campbell \textit{et al.}, 1991), or explained root proliferation ability as a consequence of differences in other traits, such as species’ growth rates (Aanderud \textit{et al.}, 2003).

One of the most influential hypotheses to explain variation in root proliferation is the foraging scale–precision hypothesis proposed by Campbell \textit{et al.} (1991), stating that there is a trade-off between the spatial scale over which species forage for resources, and the precision with which they are able to forage for resource hotspots. They proposed this trade-off as a potential explanation for the coexistence of species in communities, since subdominant species that might otherwise be competitively excluded could persist by foraging more effectively for small patches of resources missed by the dominant species. In this initial ‘scale–precision trade-off’ hypothesis, Campbell \textit{et al.} (1991; and many subsequent workers) defined foraging precision as the relative ability of species to proliferate roots in nutrient-rich soil patches. As a sign of the influence of this hypothesis, it has been cited over 130 times as of October 2007.

In a recent comparative analysis, two of us (Kembel and Cahill, 2005), confronted existing hypotheses explaining variation in below-ground foraging ability with data from numerous published root foraging studies, finding no evidence to support many of the hypotheses, including the scale–precision trade-off hypothesis. This refutation of an influential hypothesis led another two of us (de Kroon and Mommer, 2006) to discuss the prospects for future development of ideas and hypotheses related to the links between below-ground foraging plasticity, plant fitness and community structure. More recently, Grime (2007) presented his viewpoint that the scale–precision trade-off remains a useful and empirically supported framework for understanding the role of resource foraging in structuring communities, and that the scale–precision trade-off hypothesis was meant to apply only in certain habitats.

Here, all four of us respond to Grime’s (2007) combined critique of both Kembel and Cahill (2005) and de Kroon and Mommer (2006), and we suggest avenues for future research that could increase general understanding of the impact of plant foraging and plasticity on individual plant fitness and community structure.
fitness and community structure. In particular, we provide a detailed meta-analysis of published studies testing the validity of the scale–precision trade-off hypothesis, explaining why significant trade-offs may be found in datasets with a limited number of species, while there is no correlation in the community overall. Next we ask where foraging precision and plant responses to soil heterogeneity fit in trait-based plant strategy schemes, providing the first step of a new, and empirically supported, intellectual framework on the ecological relevance of plant foraging.

THE SCOPE OF THE SCALE–PRECISION TRADE-OFF HYPOTHESIS

Grime’s criticism of our studies was based primarily on the contention that we misrepresented the generality of the original foraging scale–precision trade-off hypothesis proposed by Campbell et al. (1991). According to Grime (2007), the scale–precision trade-off hypothesis was meant to apply only in habitats subjected to intermediate amounts of disturbance, but not in ‘habitats in which species-richness remains low either because the expression of dominance is unconstrained or because chronically low plant production or repeated disturbance reduce the importance of competition as a vegetation determinant’.

If Campbell et al. (1991) only intended their hypothesis to apply in intermediate disturbed meadow habitats, analyses of species from different habitats would not provide a valid test of their hypothesis. But Campbell et al. (1991) themselves used species from several different habitats in the study on which their scale–precision hypothesis is based; the four fast-growing and four slow-growing species they used included plants characteristic of habitats with varying productivities and disturbance regimes, including fertile soils, unproductive wasteland, infertile calcareous soils and rock outcrops.

We were certainly not the only authors to believe Campbell et al. (1991) presented the scale–precision hypothesis as broadly applicable to different habitats, as evidenced by the numerous papers citing their study and testing the hypothesis in a variety of different habitats (Einsmann et al., 1999; Farley and Fitter, 1999; Johnson and Briondini, 2001; Wijesinghe et al., 2001; Bliss et al., 2002; Rajaniemi and Reynolds, 2004). This is perhaps not surprising because Grime and colleagues have themselves interpreted the scale–precision trade-off as playing an apparently important role in structuring plant communities in general:

‘Precision [...] is higher in the species that occupy a subordinate position in the dominance hierarchy. This has led to the conclusion (Campbell et al., 1991) that there is a trade-off between scale and precision in resource foraging and that there is a genetic predisposition of dominant and subordinate roles in communities.’ (Grime and Mackey, 2002, p. 304).

Regardless of the original intentions of Campbell et al. (1991), there are two alternative interpretations of the scope and relevance of the foraging scale–precision trade-off hypothesis. On the one hand, if Grime (2007) is correct and the scale–precision trade-off hypothesis applies only to herbaceous species in intermediately disturbed, productive meadow communities, we are left with a hypothesis of limited relevance that cannot explain species coexistence in the vast majority of natural plant communities. On the other hand, if one accepts that Grime and colleagues were suggesting the scale–precision trade-off hypothesis as a general mechanism to explain the coexistence of species in plant communities, then a rigorous test of the hypothesis with data is required.

THE EVIDENCE FOR A SCALE–PRECISION TRADE-OFF

Ultimately, the question of whether there is empirical support for a scale–precision trade-off must address the fact that numerous studies have searched for foraging scale–precision correlations using differing numbers of species and different methods, and have found mixed results. Our earlier comparative analyses (Kembel and Cahill, 2005) focused on the combining of data from many different studies into a few large data sets suitable for analysis with phylogenetic comparative methods. In the present study, we explicitly test how the scale–precision correlation reported by individual studies varies with sample size in a meta-analysis framework. Meta-analyses allow the combination of results from multiple studies, while taking into account the fact that studies that include fewer species will provide a less-precise measure of the average result across studies (Gurevitch and Hedges, 1999).

Because of the variation in sample size and methods across published studies, we chose to use a meta-analysis framework to assess the overall evidence for a scale–precision trade-off using funnel graphs (Light and Pillemer, 1984), which have been widely used in meta-analyses to visualize how the result reported by a study varies with sample size. In the context of a meta-analysis, the results of individual studies can be thought of as samples from an underlying true result or effect size. If there exists a foraging scale–precision trade-off, we would expect the effect size (scale–precision correlation) reported by any individual study to converge on some negative value with increasing sample size (number of species). Individual studies with fewer species would be expected to show more scatter around the true effect size because of sampling error. This leads to a funnel-like appearance when the correlation observed by individual studies is plotted against the sample size of those studies, with variation in effect size large at small sample sizes and decreasing at larger sample sizes (Palmer, 2000).

For the meta-analysis presented here, we collected data on the scale–precision correlation and number of species used reported by previously published studies (see Table 1). In order to be included in our meta-analysis, a study must have reported the correlation coefficient between some measure of foraging scale and foraging precision. We collected data from all studies that met these criteria, after evaluating any study that cited Campbell et al. (1991) as of October 2007, as well as the studies cited by...
Kembel and Cahill (2005). In some cases, we included the scale–precision correlations calculated by Kembel and Cahill (2005) for studies that did not report the scale–precision correlation directly but for which the raw data were available.

We were able to find 12 scale–precision correlations reported in eight distinct data sources (Table 1). In several cases, individual studies reported more than one scale–precision correlation, due to the use of different measures of foraging scale within a single study. The concept of foraging scale has been interpreted in various ways. For example, Campbell et al. (1991) originally used the dominance of species (proportion of mixture biomass) in artificial communities as a surrogate measure for foraging scale, but in subsequent studies Grime has defined scale as root system size or biomass (Grime and Mackey, 2002), or has used composite indices of canopy height, lateral spread and litter accumulation (Grime, 1994) as a measure of scale. Regardless of the measure of foraging scale used, estimates of foraging scale–precision correlations were highly consistent within the same study (Table 1).

A funnel graph of all published estimates of the scale–precision correlation (Fig. 1) makes it clear that there is no evidence for a scale–precision trade-off. At small sample size, a few studies observed a significant positive or negative correlation between foraging scale and foraging precision, but all studies that have included more than ten species have found non-significant correlations between foraging scale and foraging precision. In both of the studies that report a negative scale–precision trade-off (Campbell et al., 1991; Wijesinghe et al., 2001), the trade-off seems to be driven by the inclusion of a single dominant, high-scale, low-precision species (Arrhenatherium elatius).

This meta-analysis supports our earlier cross-study comparative analysis (Kembel and Cahill, 2005), which found no evidence for a scale–precision trade-off across more than 130 plant species, both across a variety of habitats and within individual habitats. In particular, the ‘Great Plains Flora’ dataset collected by Biondini and colleagues (Johnson and Biondini, 2001) contained 59 species from a single habitat type, the grasslands of the northern Great Plains of North America, but there was no scale–precision trade-off across these 59 species (Kembel and Cahill, 2005). This dataset surely meets Grime’s (2007) criteria for the type of community in which a scale–precision trade-off should be observed, containing potentially co-occurring species from North American grasslands dominated by perennial herbaceous species. These grasslands are structured by intermediate amounts of disturbance by fire and grazing (Johnson and Biondini, 2001), and strong competitive interactions in grasslands are well documented (Wilson and Shay, 1990; Foster and Gross, 1998; Cahill, 2003).

The species used by Campbell et al. (1991) happen to be one of the subsets of the larger ISP dataset (Grime et al., 1997) for which one finds a negative scale–precision trade-off, even though across all 43 species in the ISP dataset for which root foraging scale and precision estimates have been published (Grime and Mackey, 2002) there is no relationship between foraging scale and precision (Fig. 1; see also Kembel and Cahill, 2005). To illustrate the effect of sample size on the chance of observing a scale–precision trade-off, we randomly drew subsets of species from the full 59 species’ Great Plains Flora dataset (Johnson and Biondini, 2001) and calculated the correlation between log10-transformed root foraging scale (measured as root system biomass) and root foraging precision for each random subset of species. A funnel graph of the randomly resampled data illustrates the relationship between sample size and scale–precision correlations for 50 randomly drawn subsets of species at each sample size (Fig. 2), and makes it clear that when sample sizes are small, there is a chance of finding a significant scale–precision correlation, despite the fact that there is no correlation in the full dataset.

**WHAT TRAITS ARE CORRELATED WITH ROOT PROLIFERATION?**

The evidence above confirms empirical support that foraging scale and precision are unrelated. This begs a most important question: what plant traits are associated with foraging precision, and how does foraging ability fit into existing plant strategy schemes? Root proliferation in nutrient hotspots is a conspicuous form of plant plasticity that is extremely variable among species, and it would be very

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**TABLE 1. Data sources included in a meta-analysis of root foraging scale–precision correlations**

<table>
<thead>
<tr>
<th>Reference</th>
<th>Label in Fig. 1</th>
<th>Number of species</th>
<th>Scale–precision correlation (r)</th>
<th>Foraging scale measure</th>
<th>Study duration</th>
<th>Nutrient application</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bliss et al. (2002)</td>
<td>1</td>
<td>6</td>
<td>0.17</td>
<td>Above-ground biomass</td>
<td>3-5 months</td>
<td>Soil patch</td>
</tr>
<tr>
<td>Campbell et al. (1991)</td>
<td>2</td>
<td>8</td>
<td>-0.48</td>
<td>Dominance in mixture</td>
<td>14 d</td>
<td>Continuous drip patch</td>
</tr>
<tr>
<td>Einsmann et al. (1999)</td>
<td>7a</td>
<td>8</td>
<td>0.39</td>
<td>Root mass density</td>
<td>39–130 d</td>
<td>Soil patch</td>
</tr>
<tr>
<td>Einsmann et al. (1999)</td>
<td>7b</td>
<td>10</td>
<td>0.40</td>
<td>Root length density</td>
<td>39–130 d</td>
<td>Soil patch</td>
</tr>
<tr>
<td>Farley and Fitter (1999)</td>
<td>8</td>
<td>8</td>
<td>0.73</td>
<td>Root system length</td>
<td>6 weeks</td>
<td>Soil patch</td>
</tr>
<tr>
<td>Grime and Mackey (2002)</td>
<td>9a</td>
<td>43</td>
<td>0.01</td>
<td>Height</td>
<td>14 d</td>
<td>Continuous drip patch</td>
</tr>
<tr>
<td>Grime and Mackey (2002)</td>
<td>9b</td>
<td>43</td>
<td>0.01</td>
<td>Root biomass in patch</td>
<td>14 d</td>
<td>Continuous drip patch</td>
</tr>
<tr>
<td>Johnson and Biondini (2001)</td>
<td>10a</td>
<td>59</td>
<td>-0.02</td>
<td>Height</td>
<td>60 d</td>
<td>Continuous drip patch</td>
</tr>
<tr>
<td>Johnson and Biondini (2001)</td>
<td>10b</td>
<td>59</td>
<td>0.17</td>
<td>Root system size</td>
<td>60 d</td>
<td>Continuous drip patch</td>
</tr>
<tr>
<td>Rajaniemi and Reynolds (2004)</td>
<td>11a</td>
<td>8</td>
<td>0.98</td>
<td>Root system biomass</td>
<td>107 d</td>
<td>Soil patch</td>
</tr>
<tr>
<td>Rajaniemi and Reynolds (2004)</td>
<td>11b</td>
<td>8</td>
<td>0.88</td>
<td>Root system length</td>
<td>107 d</td>
<td>Soil patch</td>
</tr>
<tr>
<td>Wijesinghe et al. (2001)</td>
<td>12</td>
<td>6</td>
<td>-0.83</td>
<td>Root system biomass</td>
<td>4–6 months</td>
<td>Soil patch</td>
</tr>
</tbody>
</table>
informative to understand how foraging ability is correlated with other plant traits (de Kroon and Mommer, 2006). Due to the logistical difficulty of measuring foraging ability across large numbers of species, and due to a focus on root densities and the lack of alternate frameworks in which to interpret variation in root proliferation among species (de Kroon and Mommer 2006), such analyses remain largely unexplored (but see Jansen et al., 2005).

One hypothesis to explain variation in root proliferation ability among species is that it is related to species’

Table 2. Traits included in a principal components analysis (PCA) of correlations among leaf and root ecophysiological traits (Tjoelker et al., 2005) and root foraging traits (Johnson and Biondini, 2001) for North American grassland species

<table>
<thead>
<tr>
<th>Trait</th>
<th>Label used in Fig. 3</th>
<th>Reference</th>
<th>Number of species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf nitrogen per unit mass</td>
<td>Leaf.$N_{mass}$</td>
<td>Tjoelker et al. (2005)</td>
<td>36</td>
</tr>
<tr>
<td>Root nitrogen per unit mass</td>
<td>Root.$N_{mass}$</td>
<td>Tjoelker et al. (2005)</td>
<td>34</td>
</tr>
<tr>
<td>Foraging precision</td>
<td>Precision</td>
<td>Johnson and Biondini (2001)</td>
<td>16</td>
</tr>
<tr>
<td>Root respiration per unit mass</td>
<td>Root.$R_{mass}$</td>
<td>Tjoelker et al. (2005)</td>
<td>36</td>
</tr>
<tr>
<td>Leaf nitrogen per unit area</td>
<td>Leaf.$N_{area}$</td>
<td>Tjoelker et al. (2005)</td>
<td>36</td>
</tr>
<tr>
<td>Leaf respiration per unit mass</td>
<td>Leaf.$R_{area}$</td>
<td>Tjoelker et al. (2005)</td>
<td>32</td>
</tr>
<tr>
<td>Relative growth rate</td>
<td>RGR</td>
<td>Johnson and Biondini (2001)</td>
<td>16</td>
</tr>
<tr>
<td>Leaf respiration per unit area</td>
<td>Leaf.$R_{area}$</td>
<td>Tjoelker et al. (2005)</td>
<td>32</td>
</tr>
<tr>
<td>Specific leaf area</td>
<td>Leaf.SLA</td>
<td>Tjoelker et al. (2005)</td>
<td>36</td>
</tr>
<tr>
<td>Root nitrogen per unit length</td>
<td>Root.$N_{length}$</td>
<td>Tjoelker et al. (2005)</td>
<td>34</td>
</tr>
<tr>
<td>Specific root length</td>
<td>Root.SRL</td>
<td>Tjoelker et al. (2005)</td>
<td>36</td>
</tr>
<tr>
<td>Root respiration per unit length</td>
<td>Root.$R_{length}$</td>
<td>Tjoelker et al. (2005)</td>
<td>36</td>
</tr>
<tr>
<td>Leaf $A_{area}$</td>
<td>Leaf.$A_{area}$</td>
<td>Tjoelker et al. (2005)</td>
<td>36</td>
</tr>
<tr>
<td>Biomass in heterogeneous vs. homogenous soil</td>
<td>BioHetHom</td>
<td>Johnson and Biondini (2001)</td>
<td>16</td>
</tr>
<tr>
<td>Leaf water use efficiency</td>
<td>Leaf.WUE</td>
<td>Tjoelker et al. (2005)</td>
<td>36</td>
</tr>
<tr>
<td>Root longevity</td>
<td>Root.Longevity</td>
<td>Tjoelker et al. (2005)</td>
<td>32</td>
</tr>
<tr>
<td>Leaf photosynthetic nitrogen use efficiency</td>
<td>Leaf.PNUE</td>
<td>Tjoelker et al. (2005)</td>
<td>36</td>
</tr>
<tr>
<td>Leaf longevity</td>
<td>Leaf.Longevity</td>
<td>Tjoelker et al. (2005)</td>
<td>14</td>
</tr>
<tr>
<td>Root C:N ratio</td>
<td>Root.C:N</td>
<td>Tjoelker et al. (2005)</td>
<td>34</td>
</tr>
<tr>
<td>Leaf C:N ratio</td>
<td>Leaf.C:N</td>
<td>Tjoelker et al. (2005)</td>
<td>36</td>
</tr>
</tbody>
</table>
growth rate and associated traits (Fransen et al., 1999; Aanderud et al., 2003). Fast-growing species may occupy high-nutrient patches more rapidly, leading to a higher measured foraging precision of these species in short-duration studies (Fransen et al., 1999). In other words, it is possible that most species are able to proliferate roots in nutrient patches (Berendse et al., 2007), and the main source of variation in measured foraging precision among species is actually due to differences in growth rate. Conversely, fast-growing species might quickly fill the entire soil volume in a small pot experiment, leading to a lower measured foraging precision in studies of longer duration. Empirical evidence for these patterns has been found, with longer-duration studies tending to have lower measured foraging precision (Kembel and Cahill, 2005). When root densities are evaluated after a given period of growth, fast-growing species tend to have higher measured foraging precision within a study (Aanderud et al., 2003).

The increasing availability of trait data across species may allow us to determine where plasticity and foraging ability fit into various plant functional trait classification schemes, but currently there are few large comparative trait data sets that include measurements of foraging ability. Surprisingly, while the ISP dataset (Grime et al., 1997) remains one of the most comprehensive measurements of plant foraging and plasticity across large numbers of species, there has been little discussion of the plant traits other than foraging scale that are correlated with root foraging precision in this data set.

The other large comparative data set on root foraging ability is the Great Plains Flora data set (Johnson and Biondini, 2001), which contains data on a number of foraging-related traits including precision, plant biomass response to growth in heterogeneous soil (the ratio of plant biomass when grown in soils with the same amount of nutrients distributed in a heterogeneous versus homogenous pattern; Kembel and Cahill, 2005), and growth rate for 59 species common in North American grassland habitats. Due to an overlap in study species, we were able to combine data on root foraging ability (Johnson and Biondini, 2001) with a published dataset of leaf and root ecophysiological traits for 39 North American grassland species (Tjoelker et al., 2005), with a subset of 16 species included in both studies.

We summarized trait correlations using a principal components analysis (PCA) based on eigen-analysis of the pairwise correlation matrix incorporating all data points from the two studies. This method maximized sample size, but since the trait correlation matrix itself was eigen-analysed, the positions of individual species on the resulting PCA axes were not calculated. Sample sizes for each pairwise correlation varied depending on the number of species for which data were available (Table 2). All traits were log$_{10}$(x + 1)-transformed prior to correlation analysis, and a visual inspection of the pairwise trait relationships did not detect any outliers.

The first two axes of the PCA explained 61 % and 19 % of the total variation in foraging and ecophysiological traits (Fig. 3), corresponding to the major patterns of pairwise trait correlations found in the combined data set. The major axis of trait variation among these temperate grassland species was a gradient of species with high root foraging precision, high leaf nitrogen concentration, high leaf/root respiration rates per unit mass, short-lived tissues and relatively high relative growth rates (RGR), versus those with the opposite set of traits. The second major independent axis of trait variation separated species with a positive response to growth in heterogeneous soils, higher instantaneous photosynthetic rates ($A_{\text{max}}/A_{\text{area}}$) and specific root length (SRL), and roots with low nitrogen concentrations and respiration rates per unit length from those with the opposite set of traits.

It is remarkable that precision correlated strongly and positively with root nitrogen concentration and respiration per unit mass, as it has been suggested that root internal nitrate concentration inhibits localized root branching (Zhang et al., 1999), a morphological response that underlies foraging precision. These results provide further support for the idea that foraging precision is correlated with a suite of traits related to plant growth rate, as part of the set of ‘fast’ leaf and root traits previously described by plant resource-economics strategy theory (Diaz et al., 2004). Across thousands of plant species from around the globe, there are consistent patterns of trait correlations and trade-offs related to the resource uptake strategies of species (Wright et al., 2004). The ‘fast’ end of the plant resource-uptake strategy spectrum represents species with relatively high instantaneous resource-uptake rates, short-lived leaf and root tissues with high nitrogen concentrations, and a suite of other traits such as high specific leaf area and relatively thin, poorly defended tissues.
The independence of precision and response to growth in heterogeneous soil confirms earlier conclusions (Kembel and Cahill, 2005) that despite the fact that root proliferation has been explained as an adaptation to increase resource uptake from patchy soils, the ability to place roots selectively in nutrient hotspots is a poor predictor of ability to acquire these patchy resources and convert them into plant growth. This result suggests that there are alternative acquisition mechanisms, in particular plastic nutrient uptake rates per unit of root length (Jackson et al., 1990). Consistent with this analysis, it has been suggested that this physiological plasticity is particularly important for species with slow growth rates and long-lived roots (Crack and Grime, 1987; Hutchings and de Kroon, 1994). Physiological responses are under-rated and under-studied in root foraging studies, and may play decisive roles both in the short term (Jansen et al., 2006) and the long term (Fransen and de Kroon, 2001). Clearly, there is a need not only to examine correlations between foraging precision and other plant traits, but to expand our notion of what traits might be important in determining the resource foraging ability of plants.

CONCLUSIONS

The pioneering study by Campbell et al. (1991) was one of the first attempts to link plant resource foraging to species coexistence and community structure, and was extremely important in focusing our attention on the links between resource foraging, plasticity and community structure. Unfortunately, at the moment our understanding of how plasticity and differential foraging ability affect community structure remains at a speculative stage. The comparative analyses of Kembel and Cahill (2005) along with the meta-analysis presented here make it clear that there is no empirical evidence for a scale–precision trade-off. In order to understand the importance of resource foraging and plasticity for plant fitness and the structure of plant communities we have suggested broadening our perspective and relating root plasticity to a multitude of other plant traits (de Kroon and Mommer, 2006).

In this study, we have taken a first step towards this goal by examining the relationships between root foraging and a range of ecophysiological and morphological traits, finding that root foraging precision seems to form part of a suite of traits related to rapid growth rate and the ‘fast’ set of resource-economic leaf and root traits (Wright et al., 2004). Our analysis is arguably the first attempt to relate plasticity to the traits that are now being intensively studied in the context of plant resource economy. This is remarkable given the ubiquity of within-habitat resource heterogeneity and phenotypic plasticity in plant morphological and ecophysiological traits (Ackerley et al., 2000; Sultan, 2000). By placing foraging precision as well as plasticity in resource uptake and allocation in the context of resource-economy strategies, it should be possible to develop and test predictions about how resource foraging strategies vary along environmental gradients (Grime, 1994) and affect plant fitness and community structure.
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