VIEWPOINT

The Scale–Precision Trade-off in Spacial Resource Foraging by Plants: Restoring Perspective

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• Background and Aims From the results of a comparative study using quantitative standardized assays of the scale and precision of responses of root and shoot systems to resource patchiness, Campbell et al. (1991; *Oecologia* 87: 532–538) proposed a mechanism of species coexistence in herbaceous communities involving a dynamic equilibrium between, respectively, the coarse- and fine-scale foraging of dominant and subordinate species. The purpose of this paper is to reject a recent assertion that with respect to root systems the scale–precision hypothesis has been falsified.

• Discussion and Conclusion Reference to the original papers confirms that the scope of the hypothesis was confined to circumstances (eg. mown meadows) where the vigour of potential dominants is restricted by intermittent removal of biomass. This qualification in the original hypothesis is a crucial omission from the meta-analysis conducted by Kemel and Cahill (2005; *American Naturalist* 166: 216–230). The original papers also contain examples that illustrate the operation of forms of selection that prevent the development of precise foraging below ground; these also appear to have escaped the attention of recent participants in this field of research.

Key words: Resource foraging, scale/precision trade-off, nutrient supply.

INTRODUCTION

Although individuals of most plant species remain confined to the same local patch throughout their lives, this need not prevent the development of ecological theories that resonate strongly with those used to comparing the resource foraging activities of animals. A common approach is possible because, for both animals and plants, alternative foraging behaviours can be examined by measuring net resource gain and fitness under controlled conditions of resource provision. Viewed in the context of such cost–benefit analyses, it is of little consequence that foraging in some (but not all) animals is achieved by wide-ranging locomotion, whereas most vascular land-plants forage locally and unobtrusively by growth processes that respond to changing patterns of resources and bring about a relocation of the absorptive surfaces of the plant both above and below ground.

In order to obtain reliable and relevant information on the ways in which plant foraging behaviour varies across species it has been necessary to develop techniques that allow accurate measurements of the reactions of root and shoot systems when these are exposed to controlled patchiness in resource supply. Particular difficulties arise in assays of root foraging for mineral nutrients. Controlled patchiness in mineral nutrient supply can be maintained by the use of partitions, but these do not allow a realistic simulation of the circumstances in which the root system may sustain mineral nutrient capture by local extensions that facilitate ‘escape’ from the depletion zones that are a common feature of the rhizosphere (Bhat and Nye, 1973; Drew et al., 1973). An alternative method involving the creation of nutrient patches without the use of partitions and first described in this journal (Campbell and Grime, 1989) has the following advantages.

1. Use of a continuous drip-feed of nutrient solution at four equidistant radii into a column of freely draining sand creates four geometrically exact quadrants, each of constant dimensions and uniform chemistry from top to bottom of a cylindrical container.

2. Planting of a freshly germinated seedling at the central meeting point of the four quadrants ensures that regardless of initial seedling size and root morphology there is equal access to the four quadrants.

3. The drip-feed system permits an initial phase during which mineral nutrient supply can be identical in the four quadrants, simulating the experience of an establishing seedling. After a standard time, depletion zones resembling those arising from encroaching root systems of neighbouring established plants can be introduced to half of the rooting volume by severely reducing the concentration supplied to an opposite pair of quadrants. At this point half of the containers can be harvested to measure the dry weight of root in each quadrant. The remaining replicates can be harvested after a further period of growth, permitting a calculation of the increment of root growth in depleted and undepleted quadrants.

The drip-feed method was used in an assay of root foraging characteristics that formed an important part of a large-scale experimental screening programme (the Integrated Screening Programme, ISP) measuring a wide range of plant traits in forty-three common plants of the Sheffield region in north-central England. The results of
this whole study have been published (Grime et al., 1997) but the parts relating specifically to root (and shoot) foraging were judged to be sufficiently novel and interesting to merit more detailed and early presentation. There were three additional reasons for special attention to the foraging data from the ISP.

(1) The foraging components of the ISP required the constant attention of an experienced technician over a period of three and a half years. Despite the effectiveness of the techniques used it was therefore considered unlikely that foraging studies with the scale and precision achieved in the ISP would be undertaken in many other laboratories.

(2) A consistent feature of the ISP results was a correlation between the foraging characteristics of the root and shoot systems, a feature in direct conflict with several published hypotheses proposing an evolutionary trade-off in allocation of mass between root and shoot (e.g. Iwasa and Roughgarden, 1984; Tilman, 1985).

(3) On the basis of field surveys and experimental studies, theories had begun to develop (Grime, 1987) implicating genetic constraints on plant foraging behaviour as forces influencing, under specified conditions, the dominance hierarchy in plant communities.

A consequence of the decision to publish early the results of the root and shoot foraging tests in the ISP has been the appearance of a series of papers (Campbell et al., 1991a, b; Grime et al., 1991; Grime, 1994, 1998; Grime and Mackey, 2002) that, among several objectives, has explored the significance of one particular feature present in these data – evidence of a trade-off between the scale and precision of foraging. This research has recently culminated in a theoretical framework (Grime et al., 2007) in which the trade-off is recognised as one of five mechanisms capable, in specific circumstances, of sustaining co-existence in species-rich plant communities. Against this background it was a matter of surprise when two papers (Kembel and Cahill, 2005; de Kroon and Mommer, 2006) were published, each expressing the opinion that the notion of a trade-off between the scale and precision of foraging by root systems had been falsified.

The purpose of this paper is to examine the validity of this conclusion in the light of two sources. The first consists of publications by those who conducted the ISP foraging experiments, whilst the second refers exclusively to Kembel and Cahill (2005) and de Kroon and Mommer (2006).

SCALE–PRECISION TRADE-OFFS IN THE ISP

The 43 herbaceous species included in the ISP were chosen to represent common species from a wide range of freely draining, unshaded habitats of inland Britain. Even before the screening tests were completed on all species it was apparent that there were major differences in the scale, precision and rate with which the root and shoot systems exploited resource heterogeneity. Reference to the results of extensive field surveys and autecological profiles (Grime et al., 1988) revealed that many species-rich communities contained species that differed to a marked extent in the scale and precision of their responses to controlled patchiness of resource presentation in the ISP. There were also indications that coarse-grained (high scale) foraging was associated with the large shoot and root systems of robust, potentially dominant species, whereas fine-grained (high precision) foraging coincided with the smaller leaves and roots of plants that are rarely observed to attain dominance and appeared to rely upon exploitation of small patches of resources between the depletion zones created by the dominants. This led to the hypothesis that a trade-off between the scale and precision of resource foraging might contribute to the mechanisms that permit species of very different stature to coexist in some plant communities.

Before proceeding further it is essential to define as closely as possible the scope of the scale–precision hypothesis tested in the ISP results. Trade-off theories form a continuum, including at one extreme all living organisms (e.g. MacArthur and Wilson, 1967) and at the other referring exclusively to plants exploiting a narrow range of specialized habitats (e.g. Landsberg et al., 1999). The following quotations illustrate the limitations of applicability that were applied to the hypothesis tested in the ISP foraging papers.

‘The capacity to make these plastic adjustments might be expected to be particularly critical where competition is important in vegetation. Here it is helpful to bear in mind that competition does not uniformly lower the resource supply either above or below ground. Instead there is a local depletion of nutrients and water in the immediate vicinity of individual roots and light under individual leaves.’

Campbell et al. (1991a)

‘At one extreme, Arrhenatherum elatius appears to monopolize resource capture within a large volume of soil volume by the development of an extensive root system which includes large arterial roots. Such “coarse-grained foraging” is clearly incompatible with the precise location of dry matter in undepleted zones; by comparison, the smaller and predominantly fine-rooted systems of subordinates, such as Campanula rotundifolia, exhibit “fine-grained foraging” in which there is a more intensive and precise exploitation of a localised part of the resource mosaic.

This interpretation is clearly compatible with those theories of vegetation dynamics (Grime 1973, 1987; Grubb, Kelly and Mitchley 1982) which recognize the mechanism of species coexistence in perennial herbaceous communities as an oscillating equilibrium between (1) the tendency, in the absence of vegetation disturbance, for potential dominants to mobilize resource capture and drive the system towards monoculture, and (2) the tendency, following disturbance and debilitation of potential dominants,
for subordinates to generate diversity by exploiting individual parts of the resource mosaic.

Grime et al. (1991)

I submit that these quotations make it abundantly clear that the hypothesis under test does not apply to plants in general but has specific relevance to the wide range of plant communities (e.g. mown meadows) in which intermittent biomass removal (disturbance) limits the expression of dominance and creates opportunities for temporary expansions of subordinate species that, at other times when dominants attain large stature, retain a foothold by precise foraging in resource-rich microsites. It is clear therefore that the scale–precision hypothesis does not apply to the large number of 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 vegetational determinant.

If we now turn to the published results of the ISP foraging tests we see evidence of two kinds, each confirming the specific relevance of the scale–precision predictions to circumstances of high species-richness maintained by intermittent biomass removal. In Campbell et al. (1991a), a rather severe test was conducted of the ability of the root and shoot foraging tests to predict the composition of a plant community created on a fertile medium by sowing an equiproportional seed mixture of eight species and allowing development in glasshouse conditions for 16 weeks. The results confirmed the ability of both root and shoot foraging data and species growth rate to predict the status of each of the species in the experimental community, and were consistent with the idea of a trade-off between the scale and precision of foraging. It is interesting to note that although the eight species were deliberately chosen to include four fast-growers and four slow-growers (Grime and Hunt, 1975), this distinction did not obscure a clear hierarchy within both the fast-growers and the slow-growers that was correlated in each case with the independently derived foraging characteristics. No mention of this experiment is made in the review of de Kroon and Mommer (2006).

When the programme of ISP foraging tests was completed, analyses could be carried out using the whole dataset (Grime, 1994; Grime and Mackey, 2002) to examine on a completed, analyses could be carried out using the whole dataset (Grime, 1994; Grime and Mackey, 2002) to examine on a wider basis the factors influencing the precision of foraging by shoots and roots. These reports confirmed that potential dominants of herbaceous communities, defined by reference to canopy height, lateral spread and litter accumulation (Grime, 1973) had lower foraging precision than most of their associated subordinates. However, it was also apparent that some plants of small stature and limited ability for coexistence with potential dominants exhibited low precision in foraging that could be traced to trade-offs involving other powerful selective forces affecting root and shoot development. Hence, for example, it was suggested that in some species of droughted habitats (e.g. *Pilosella officinarum*) high precision of root foraging was precluded by the early development of a tap-root. In the rather different circumstances of permanent pastures it was concluded that precision of both root and shoot foraging in some of the ISP species had been forfeited under the intensive selection pressures associated with continuous defoliation, trampling and poaching; in these plants, adventitious roots and intercalary shoot meristems confer resilience at the cost of the mechanisms required for precise foraging in a patchy environment.


In the short comment that is necessary under this heading it is useful to be reminded of the conclusions drawn by the authors of these two papers.

‘From an ecological perspective, it appears that longstanding theories of the controls of interspecific variation in root foraging are incorrect. We found no empirical support for a trade-off between foraging scale and precision ... ecological research must move beyond the study of root responses of isolated plants and focus on the functional consequences of root foraging ability under more natural conditions in multispecies communities.’

Kembel and Cahill (2005)

‘The results of Kembel and Cahill (2005) call for a reconsideration of scale and precision as general measures of foraging ability in plants...The results of Kembel and Cahill (2005) leave much of the variation in root proliferation among species unexplained.’

de Kroon and Mommer (2006)

From these statements it is clear that both sets of authors believe that the scale–precision hypothesis of species coexistence in plant communities of Campbell et al. (1991a) has been falsified. It is undoubtedly true that the meta-analysis of Kembel and Cahill (2005) appears to have falsified a hypothesis, but it is one that bears little resemblance to that contained in Campbell et al. (1991a). In part, this miscarriage appears to have arisen from the false premise that we proposed that the scale–precision trade-off extends across the entire spectrum of vascular plants and their communities. It is difficult to understand how such a misunderstanding could arise, since each of the six papers emanating from the foraging component of the ISP specifically associates the scale–precision hypothesis with circumstances where intermittent disturbance provides the non-equilibrium conditions within which scale and precision can each enjoy a selective advantage in alternating sequence. Here one example will suffice.

‘It seems likely that there is an oscillating equilibrium between (1) the tendency, in the absence of perturbation, for potential dominants to monopolize resource capture and drive the community toward monoculture and (2) the tendency, following perturbation and temporary debilitation of the dominants, for subordinates to generate diversity by exploiting local parts of the resource mosaic. Crucial to this hypothesis is the
idea that during phases in which dominance is strongly expressed, the survival of subordinate species will depend on their ability for precise location within any patches of sunlight and mineral nutrients unexploited by the coarse-grained resource interception of the dominants.'

Grime (1994)

As explained earlier, our papers also include references to circumstances (for example, those of drought and of continuous grazing and trampling) where optimal foraging is secondary in importance to the development of traits that reduce the precision of foraging but increase fitness under the impact of other countervailing selective factors. The omission of references to these qualifications cannot be excluded from any assessment by the editors, reviewers and readers of the distorted presentations of the scope of the scale–precision hypothesis that was permitted in two widely circulating journals. However, the ‘falsification’ perspective was also crucially dependent upon a policy of ignoring two other published features of the ISP results. The first of these was the fact that the patterns in scale and precision in root foraging had been found to closely match the results from a comprehensive set of analogous tests on the shoot system. The second refers to the call of Kembel and Cahill (2005) that ‘ecological research must move beyond the study of root responses of isolated plants and focus on the functional consequences of root foraging ability under more natural conditions in multispecies communities’. This was in fact provided in Campbell et al. (1991a), where it was found that the results of root and shoot foraging tests ‘on isolated plants’ accurately predicted the status achieved when the same species were grown together in ‘a multispecies community’.

CONCLUSIONS

Meta-analysis or metamorphosis?

In this short paper the primary concern has been to draw attention to the curious progress of an idea that began its life as a tightly defined hypothesis and experimental validation (Campbell et al., 1991a) only to be threatened 14 years later with oblivion in the dustbin of ecological history. How did this happen and is this an appropriate outcome?

First, it is interesting to observe that our experimental results testing the value of variation in the scale, precision and rate of root and shoot foraging data as predictors of the composition of a multispecies community remain unrepeated and unchallenged. Nor is there any convincing argument falsifying our conclusion that a trade-off between scale and precision is crucial to an understanding of how intermitent biomass removal sustains coexistence between dominant and subordinate members of meadow communities.

Second, it is evident that our discovery within the list of ISP species of plants in which the benefits of precise foraging had, of ecological necessity, been sacrificed by the development of traits essential to other aspects of fitness in particular habitats apparently did not deter some ecologists from unreasonable expectations of the scale–precision theory. Did Hodge et al. (1998), for example, really expect that a scale–precision trade-off would be more important in woodland herbs than adaptations relating to seasonal shade, emergence from tree litter and the impacts of tree roots?

I conclude that the meta-analysis of Kembel and Cahill (2005) and the review of de Kroon and Mommer (2006) completed a sequence closely akin to the children’s game of ‘Chinese Whispers’ in which a message gradually loses its identity and assumes a new one as it passes by word of mouth around a circle of participants. We did not suggest, or even whisper, that all plants were subject to a trade-off between scale and precision in their mechanisms of resource capture.

Scale and precision in ecological research

In this paper I have tried to restrict attention to a scientific issue that threatens the survival and implementation of an idea that, in my view, has practical relevance to our understanding of how species-richness is maintained in some plant communities. However, the short history of the scale–precision hypothesis cannot be detached completely from a much older phenomenon concerning the way ecologists conduct their research. For some time (Grime, 1965) I have been convinced of the value of large-scale surveys of organismal traits to establish on a statistical basis the patterns of trait variation and association that reflect major trade-offs and axes of functional specialization. At the present time this activity, particularly as it applies to vascular plants, is beginning to achieve the momentum and consensus necessary for scaling up to an understanding of community and ecosystem functioning and management. Against this background, the scale–precision saga recounted in this paper underlines the need to clearly establish a hierarchy with respect to the scale at which patterns and trade-offs are applicable.

In order for patterns of functional specialization and suspected trade-offs to be securely assimilated into ecological theory these need to be translated into a mechanistic framework. This means that ecologists with narrower frames of reference and objects of study have a vital role to play. This, in turn, brings the risk of misunderstandings as scientists dedicated to a contrasted mix of scale and precision in their working methods and philosophies interact. Resolving the usefulness and limits of the scale–precision hypothesis will require a tolerant dialogue.

LITERATURE CITED


Hodge, A; Stewart, J; Robinson, D; Griffiths, BS; Fitter, AH. 1998. Root proliferation, soil fauna and plant nitrogen capture from nutrient-rich patches in soil. *New Phytologist* 139: 479–494.


