Opinion

# Focusing the metaphor: plant root foraging behaviour

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**Many authors assert that plants exhibit complex behaviours which are analogous to animal behaviour. However, plant ecologists rarely root these studies in a conceptual foundation as fertile as that used by animal behaviourists. Here we adapt the optimality principles that facilitated numerous advances in the study of animal foraging behaviour to create one possible framework for plant foraging behaviour. Following the traditions of animal foraging ecology, we discuss issues of search and handling in relation to plant root foraging. We also develop a basic plant-centered model that incorporates modular growth and foraging currencies relevant to plant growth. We conclude by demonstrating how this new foundation could be adapted to address five fundamental questions in plant foraging ecology.**

## Plant behaviour

Standard definitions of 'behaviour' refer to the action or reaction of an individual to an event or stimulus. Although behaviour is typically considered a feature of animals, this definition does not exclude the responses of other organisms, including plants [1,2]. This broad definition of behaviour has encouraged plant ecologists to investigate areas traditionally tackled by animal behaviourists, including territoriality [3], kin selection [4–6], mate choice [7,8], sexual conflict [9,10], nonrandom foraging [11–15], interspecific communication [16–19] and game theory [18–22]. This idea that plants behave in ways that are similar to animals has generated substantial debate, often centered on the term 'behaviour' and whether it can occur without cognition [4–6,18–20]. We do not address this here and instead assume plants do exhibit behaviour, and seek to integrate plant behaviour within the broader discipline of behavioural ecology. Our definition of behaviour assumes that phenotypic plasticity in plant growth is produced by stimuli for which alternative responses would produce differential fitness. We label these alternative responses as 'behaviour,' although the word used is not critical to our argument. Although plant behavioural ecology is empirically rich, we believe it has lacked a common conceptual foundation to integrate the growing number of mechanistic studies [15].

In this article, we use the specific case of plant root foraging behaviour to show that plant behaviour can be cast in a more general context of behavioural ecology. We propose that optimality theory might serve to unite many seemingly discrete empirical studies, just as it has done in animal behavioural ecology. We will focus primarily on the ultimate causes of root foraging behaviour (Box 1), because the proximate causes of root foraging are reviewed elsewhere (Box 2) [12,23–29]. Also following the traditions of animal behavioural ecology, we focus on the behaviour of individuals rather than interspecific variation (Box 1). Our discussions are centered on the 'general' biology of plants and animals, but this does not rule out the potential for 'atypical' taxa to provide critical insights. We begin our discussion of root foraging by contrasting aspects of the basic biology of plants and animals, which will necessarily affect how plants exhibit behaviour.

## How do plants and animals express behaviour?

Let us begin with a common metaphor, that plant roots growing in soil are analogous to a foraging animal [2,29] (Figure 1). At a superficial level, this seems reasonable; both organisms search for, capture and handle resources. But if you look deeper, this analogy lacks focus. In general, an animal consumes prey that provide energy and essential nutrients, whereas plant roots capture mineral nutrients and water which are used to construct organs that capture energy from the sun. An individual animal is made up of a single foraging unit with one mouth that can perform a limited number of behaviours at once. An individual plant is built from a series of repeating foraging units which can each perform different behaviours simultaneously [30]. A moving animal leaves only a trail, but a plant 'moves' by creating or elongating cells behind the advancing root tip, leaving behind semi-permanent tissues which require ongoing maintenance.

Two differences between plants and animals stand out as most strongly impacting the development of a conceptual foundation for plant foraging ecology: (i) modularity – generally, plants forage by growing new organs that can occupy many places simultaneously, whereas animals forage in one place at a time [30]; and (ii) currency – because plants and animals differ in the mechanisms of energy capture, the 'currencies' they spend and receive from foraging also differ [31]. Despite these differences, plants should still be expected to behave in ways that enhance fitness, suggesting that broad concepts from animal-based optimality models might provide an initial foundation for the study of plant behaviour. In the sections that follow, we will expand these ideas and use well-established concepts from the animal foraging literature to develop a model that takes into account these details of plant biology.

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### Box 1. Types of behavioural questions

The idea that plants might exhibit complex responses to their environment is at least as old as Darwin [63]; however, the formal study of plant behaviour has only become common in recent years [1,2]. By contrast, detailed study of animal behaviour began about a century ago, with two separate paradigms emerging. In Europe, ethologists focused on mechanisms of innate behaviour and evolutionary history. In North America, the emergence of operant psychology emphasized learned responses and plasticity. These disparate traditions promoted answers to what were subtly different forms of questions, sometimes causing fruitless debate. Mounting semantic confusion was alleviated with the identification of two kinds of behavioural questions: proximate and ultimate [43,64]. Questions about causation and development provide proximate answers about *how* a given behaviour comes about in the lifetime of an organism. Questions about evolutionary history and functional significance provide ultimate explanations about *why* a given behaviour exists in the repertoire of a species. These two types of questions are known as Tinbergen's questions, and they continue to define the scope of modern behavioural investigations [65] as well as refine the approaches to new behavioural subdisciplines [66]. Plant behaviourists have not generally framed their questions this way, but doing so might avoid similar confusion in the development of plant behavioural research programs.

Questions about behaviour can also be asked at different taxonomic levels [43]. Behavioural research can seek to understand the behaviour among individuals within a species, or to make broad comparisons in the behaviours among species. Investigations at the level of the individual can reveal the types of behaviours that are possible and details about the adaptive and ecological value of a given behaviour. Only once this is understood can one meaningfully compare behaviours among species. We believe that plant ecologists have generally been interested in comparing among species, rather than understanding the basic behaviours of plants at the level of the individual.

## How is animal foraging described mathematically?

The foundation of most animal foraging models is strikingly similar. Solitary animals are generally expected to perform behaviours which maximize energy intake per unit time [32–38]. This rate can be expressed mathematically (notation follows Refs [36,37]), where $E$ is the energy intake during a feeding period of length $T$. Typically, $T$ is subdivided into search and handling times, $T_S$ and $T_H$, respectively. Thus, the net rate of energy intake can be expressed as

$$\frac{E}{T} = \frac{E}{T_S + T_H}. \qquad \text{[Equation 1]}$$

To accommodate specific questions about animal foraging, this basic idea is modified to incorporate parameters such as prey abundance, patch location or habitat quality [34–39].

Two seminal questions emerged from this basic model: how should predators choose prey, and how much time and effort should foragers spend in patches? These questions have been addressed with several optimality models [38–44]. Prey choice models generally compare the profitability of different prey relative to the costs associated with foraging (Box 3). These models typically demonstrate that the costs of specialization decrease as the relative abundance of favoured prey increases [34,36]. Patch use models ignore prey quality and recognize that prey are often aggregated into patches (Box 4). Patch use models predict that organisms should spend more time in a patch when travel time among patches increases, average resource density within patches increases or when overall habitat quality is low [35].

## Toward a framework for optimal plant foraging

If heterotrophic animals maximize the rate of energy gain, what should modular, autotrophic foraging plants be expected to maximize? In the sections that follow, we will modify the structure and components of Equation 1 to enhance its applicability to plant foraging. The equations we generate are simple, and not mathematically derived from each other. Instead, they are meant to serve as signposts that crystallize our logic rather than a mathematical proof. We do not claim that our model will be the endpoint for theoretical development of plant foraging behaviour, and instead hope that our model will encourage more research in this direction.

## The importance of plant modularity

Plant bodies are constructed from a series of repeating units that occur at multiple scales [30]. At the larger scale, genetically unique plants (genets) can consist of clonal daughter plants (ramets). Depending upon the species and environmental conditions, ramets can live independently, or can be connected with the potential for resource sharing, division of labour, and communication [30]. A second scale of modularity involves repeating organs within the plant body (metameres), each of which includes meris-

### Box 2. Root foraging; 'why do plants bother?'

Questions about plant foraging can be divided into two general categories which parallel Tinbergen's questions about behaviour [64]: *how* do plants forage? And *why* do plants forage the way they do? We suggest that the first question has been the primary focus of plant behaviourists for the past 20 years, and many of the fundamental *how* questions have been asked and answered. By contrast, questions about *why* plants forage the way they do are less frequent in the literature and, so far, have been much harder to answer [12,13,15]. We believe that a broader conceptual framework is needed to focus this research.

*How* do plants forage? Plants possess a diversity of root responses to heterogeneity including increased lateral branching, root biomass, root length and uptake capacity [11,12,26,29,30,67]. Plants also adjust root demography and the length per unit mass of roots in response to heterogeneity [12,68,69]. In combination with root responses, clonal plants generally respond to soil heterogeneity by shortening the distance between daughter ramets and increasing the density of ramets in patches [11,67,70]. The physiological mechanisms which underpin these morphological responses are still being described, but the understanding of these mechanisms is constantly expanding [23–25,27,28]. Thus, *how* plants forage is relatively well understood.

Plant ecologists have only begun to explain *why* plants forage the way they do. Many studies have implied that plants are optimal foragers [12,14,71], but there is little experimental evidence built on this assumption [13,15] and only a handful of studies that explicitly develop optimality models for plant foraging [31,47]. We suggest that a more general framework of optimality is necessary to fully establish a subdiscipline of plant behavioural ecology. Once it is possible to express plant choices as costs and benefits, we believe that it will be easier to answer the questions related to *why* plants forage the way they do in the context of optimization.

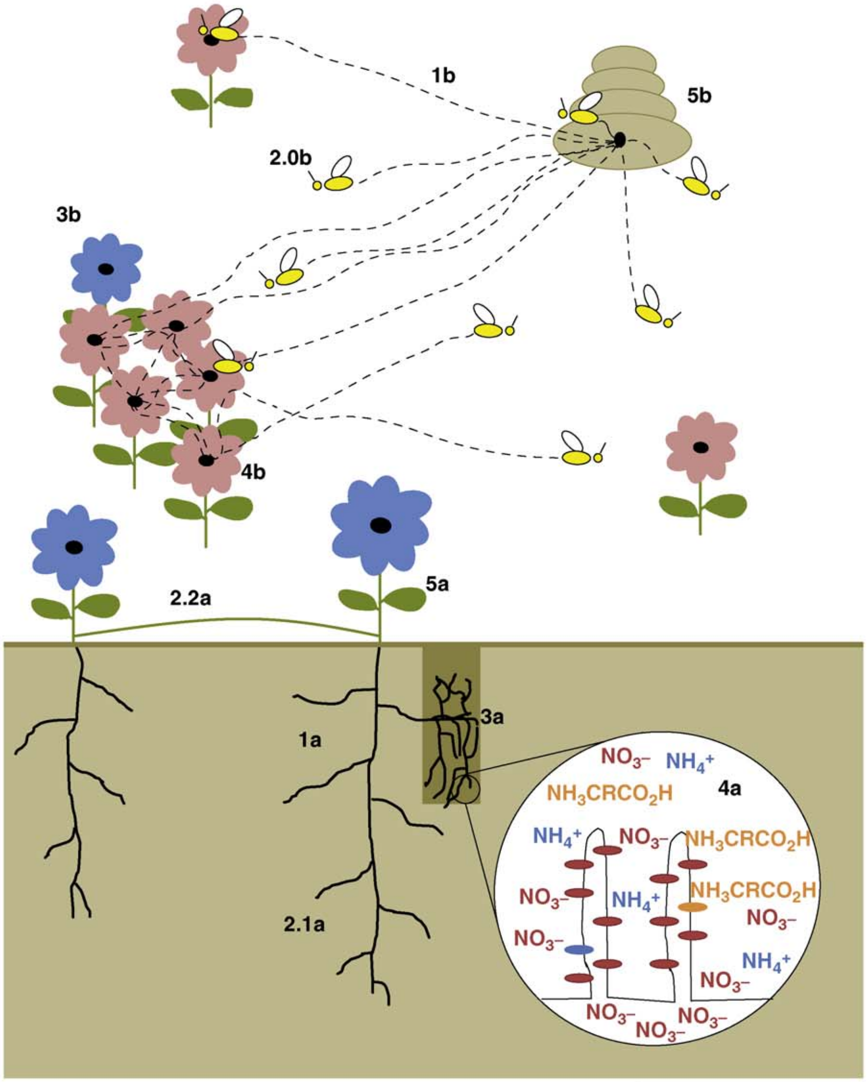

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**Figure 1**. Cartoon comparison of how plant **(a)** and social insect foraging **(b)** might be analogous. This cartoon comparison is meant to serve only as a simple way of making phenotypic plasticity in plants comparable to the well-studied foraging behaviour of animals. However, there are enough significant differences between plants and animals to make this analogy a tenuous one and this figure should therefore not be taken literally, and should be interpreted with extreme caution. Nutrient uptake in plants occurs primarily in the root tips (2.1a). Root tips move throughout the soil through increased growth and elongation of roots. Roots are attached to daughter ramets (2.2a), which move across the landscape through the growth of new physiologically connected ramets. By comparison, in a social insect colony, resource capture occurs primarily by autonomous workers (2.0b). The individual root tip and the worker have similar genetic composition to the other root tips and workers, but do not reproduce themselves. Thus, the individual foragers (i.e. roots or workers) should work to maximize the performance of the plant or the colony as a whole, rather than their own individual performance. When resources are distributed in patches, plants increase the number of root tips in a patch (3a), whereas social insects will increase the number of visits to a patch (3b). This behaviour is well documented by empirical studies in both plants and animals. When there are multiple types of a resource with different costs and benefits, organisms are expected to select among these resources in a way that maximizes benefits and minimizes costs. For plants (4a), these resources are individual forms of specific nutrients; for example, nitrogen is taken up as nitrate ($NO_3$), ammonium ($NH_4$) and various amino acids ($NH_3CRCO_2H$). These are captured through the use of a variety of uptake mechanisms (colour-coded ovals, 4a) and, in this scenario, plants preferentially uptake $NO_3$ through the use of some specific uptake mechanism (red ovals). However, these mechanisms are generally poorly understood in plants, and our hypothesis that plants should be capable of prey selection has not been empirically tested. For the social insects depicted (4b), these resources are different flowers (colour coded). In this scenario, the insects preferentially visit the pink flower species. This prey choice behaviour in animals is well documented by empirical studies. Captured resources in plants can be transported to the shoot (5a), where they influence energy capture and the production of new foraging units (roots/ramets). For social insects, captured resources are transported to the colony (5b) for consumption and eventually can influence the production of new foraging units (workers).

temic tissues [12]. Meristems contain undifferentiated cells, allowing the creation of new plant organs in different areas based on local conditions. At a finer level, individual roots contain uptake proteins, and nutrient transport pathways that influence the capture of mineral nutrients [23,28]. Through plasticity in growth among these foraging units, plants are able to capitalize on opportunities, such as canopy gaps or nutrient-rich soil patches [11–13]. One way to visualize these different levels of organization in plant bodies is to think of plants as having many ‘mouths’ spread out over large areas (Figure 1). Perhaps even more importantly, these plant mouths can act independently, even while selection acts upon the individual as a whole [30,45].

The issue of modularity poses an immediate challenge to Equation 1. Individual animals have one mouth, and there is a clear correlation between the activity of the mouth and the fitness of the organism. However, in plants, this relationship is more complicated. Like animals, plants can alter the activity of existing foraging units but, unlike solitary animals, plants can also produce new foraging units [30]. Any model of plant foraging must account for the semi-separate activities of the collective parts of plants, and it is

### Box 3. Prey choice models

When multiple prey types of varying quality are available to an organism, which prey should be consumed? Animals are expected to select the prey that maximizes energy gain per unit time. This means that prey with the highest energy content and the lowest search and handling costs should be favoured [36,37,43]. The abundance of prey will also influence prey choice.

The ideas concerning costs and benefits of prey choice can be generalized into two basic predictions of prey choice models which can be expressed both graphically and mathematically [32–37]. First, when prey can be ranked in order of their profitability, there should be some subset of prey which includes only the highest-quality prey and excludes the lowest-quality prey (Figure I). Second, the breadth of the diet will be influenced by the abundance of prey. As the abundance of high-quality prey declines, they become harder to find, increasing search costs, and lower-quality prey that were originally avoided will be included in the diet of the organism.

Plants are faced with choice about diet composition, in the form of multiple chemical forms of many essential nutrients. As in animals, these different 'prey' choices each can result in different growth rates in plants. For example, nitrogen exists in soil as nitrate, ammonium and a variety of amino acids. Plant species have maximal growth under different ratios of these different forms of nitrogen [55,56], and plants can show different growth rates or lifetime fitness when grown on a single nitrogen source [72]. These findings suggest to us that plants should be expected to actively select 'prey' in a way that is analogous to prey choice in animals. What would active choice look like in a plant? Likely it is through the use of molecule-specific uptake proteins, and transport pathways [49,72], but these proximate mechanisms are poorly understood [23,28].

Detecting prey choice in plants will require experiments which track the uptake of specific chemical forms of nutrients when they are provided at different ratios of abundance. This will also require the ability to rank the profitability of different plant prey. Plants should be predicted to focus on high-quality prey only when they are abundant and to broaden their diet to include lower-quality prey when the highest-quality 'prey' is rare.

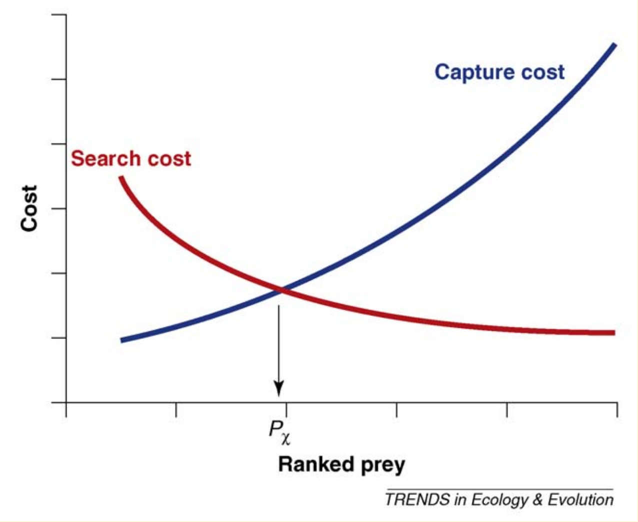

**Figure I.** Adapted from MacArthur and Pianka [33]. Change in cumulative search and capture costs for animals as diet breadth increases. In this model, prey are ranked on the x axis by the capture (handling) costs required to consume them. As diet breadth expands, less profitable prey are included in the diet and the cumulative capture cost increases (blue line). However, as more prey items are included in the diet, cumulative search cost declines because more consumable prey are encountered more frequently (red line). Optimal diet in this example is predicted by the point where the two curves intersect. In this hypothetical example, the optimal diet breadth included prey items 1 to $P_x$. Although search and handling costs cannot be separated for foraging plants, plants should still be expected to select 'prey' which minimize the overall foraging costs and maximize the overall foraging gains. This seminal model is not widely used anymore, but is still useful for describing the concept of prey choice.

unclear whether a version of Equation 1 should be applied to the whole plant or to each individual foraging unit. Insight might come from studies of social insect colonies (Figure 1).

## Modular plants might behave like an insect colony

Individuals of social insect colonies, such as the social hymenoptera, are expected to behave differently from solitary animals because the individuals who forage do not typically also reproduce [45]. In such cases, the behaviour of workers is expected to enhance colony fitness, rather than individual energy gain of workers. We suggest that foraging in plants might be similar, where selection should favour behaviours which enhance total plant fitness, rather than the performance of each and every foraging unit within the genet (Figure 1).

In our development of Equation 1, we must now consider the sum of the behaviours of all parts of the plant separately. If there are $n$ ramets, $m$ root meristems and $E_{ij}$, $T_{Sij}$ and $T_{Hij}$ are the gains or costs from the foraging activities of root $j$ on ramet $i$, then

$$\frac{E}{T} = \sum_{i=1}^{n}\sum_{j=1}^{m}\frac{E_{ij}}{T_{Sij}+T_{Hij}}. \qquad \text{[Equation 2]}$$

In Equation 2, if we assume that total foraging performance is correlated with fitness, then the fitness of the plant will include the sum of all foraging roots, across all the foraging ramets within a single genet. For simplicity, this equation also assumes that there are no interactions between the individual foraging units of a genetic clone, and we ignore units of organization smaller than individual roots (e.g. uptake proteins). This is reasonable, because many studies suggest that plant roots within an individual avoid or at least minimize self-competition [16,17] and that foraging decisions are made in the root tips [2,46]. However, the impact of interactions among foraging units within the individual could be modeled [30], and lower levels of organization such as uptake proteins could also be considered (Box 3). However, Equation 2 represents foraging costs and benefits for plants in units of currency developed for heterotrophs.

## The benefits of plant foraging are complex

For foraging animals, the currencies of energy and time make sense when fitness is limited by energy intake, and by the number of things an animal can do at once [35–39]. However, these currencies are inappropriate to describe the foraging behaviour of modular, autotrophic foraging plants. One possible solution would be to simply replace 'energy' with 'nutrients' in the numerator of Equation 2. This solution has been applied in previous attempts to apply optimal foraging models to plants [31,47,48]. However, the relationship between nutrient uptake and fitness gain is not always positive or linear for plants [49], and thus maximizing capture of a single nutrient would not necessarily maximize plant fitness. There can also be

### Box 4. Patch use models

When prey are aggregated into a mosaic of patches and patch value declines as an organism depletes it by foraging, how long should the organism remain in a given patch? This question has been addressed in animals by applying the marginal value theorem (MVT) [35] and other patch use models [38,39]. Patch use models predict that the time spent in individual patches will maximize the rate of energy gain over time [35]. Because there are costs associated with traveling between patches, both the average distance between patches and the profitability of patches influence the patch residency time of foragers (Figure I).

These two ideas concerning the costs and benefits of patch use can be generalized into three basic predictions of patch use models like the MVT. First, as the resource density of the patch increases, it takes longer for resources to be depleted to the average level of other patches. As a result, an individual should spend more effort and time in a high-quality patch compared to a low-quality patch (Figure I). Second, as travel cost between patches increases so too do costs of leaving a patch. As a result, an individual will spend more effort in a patch before moving on when patches are farther apart (Figure I). Finally, as the overall profitability of the average patch in an environment declines, organisms should spend more time and effort in each patch.

Plants are similarly faced with a patchy distribution of soil resources [11], and these resources are often depleted with increasing foraging effort [69,73]. Some of the basic predictions of patch use models have been shown for plants, and explicitly linked to patch use models from the animal literature [31,47,48,58]. For example, plants proliferate into patches of varying quality in proportion to their quality [31,74]. Similarly, foraging effort in patches can be influenced by the overall habitat quality [73]. Plants also leave patches in two ways: (i) through the senescence of roots, or (ii) by physically growing through patches and exiting out the other side. Plants have also been shown to control the timing of patch leaving as predicted by the MVT (FigureI), and will remain in high-quality patches longer than low-quality patches before leaving them through root growth and cell elongation [58]. Patch leaving through senescence of roots has not been addressed. In general, it seems that patch use behaviour in plants is strikingly similar to patch use behaviour in animals, although few authors cast their results or experiments in this light [58].

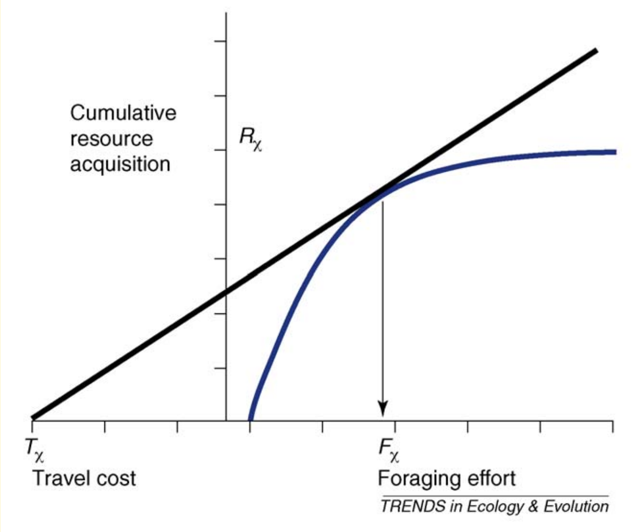

**Figure I**. Adapted from Charnov [35]. This figure shows the expected relationship between cumulative resource acquisition (blue curve), effort spent foraging in a patch and travel cost between patches. As an organism spends more effort foraging in a patch, the quality of the patch is depleted and resource acquisition eventually plateaus at some maximum level of resource acquisition ($R_x$). A tangent line (black line) drawn from the travel cost to the gain curve identifies the point where the marginal value of staying declines below the average profitability of all patches and organisms should only invest $F_x$ effort into the patch. Increasing travel cost ($T_x$) increases the amount of effort spent foraging in the patch ($F_x$). Increasing patch quality also increases the maximum amount of resources that can be extracted from the patch ($R_x$), and as a result increases the amount of effort spent in the patch ($F_x$). Although travel and handling costs are difficult to separate for plants, plants have been shown to expend effort in proportion to patch quality, and to control the timing of patch exit as predicted by patch use models designed for animals.

complex interactions among essential resources and plant fitness. For example, a given concentration of nitrogen can be limiting to plants under high phosphorus availability, but not when phosphorus itself is limiting [49,50]. Under this common scenario, maximizing the capture of any single nutrient would not necessarily maximize plant fitness.

The implications of nonlinear interacting nutrient relationships for Equation 2 are that the parameter $E_{ij}$ is too simplistic and should be replaced by some fitness generating function, $f(r_{ij})$, which describes the nonlinear benefits and interactions among the resources that limit plant growth (e.g. [51]). Although there are large numbers of essential resources for plant growth, $f(r_{ij})$ need only focus on a subset depending on the environment, species under study or the question being addressed. If we replace $E_{ij}$ with $f(r_{ij})$ in Equation 2, then

$$\frac{E}{T}=\sum_{i=1}^{n}\sum_{j=1}^{m}\frac{f(r_{ij})}{T_{Sij}+T_{Hij}}. \qquad \text{[Equation 3]}$$

In Equation 3, $f(r_{ij})$ is different from $E$ in Equations 1 and 2 because as a function it can account for the multi-dimensionality of plant mineral nutrition, converting nutrient capture into potential for energy or fitness gain [51,52]. We will leave $f(r_{ij})$ undefined at this point, and return to it after we have discussed the costs of plant foraging.

## The costs of plant foraging are complex

Animal foraging models often differentiate costs as either search or handling, which are assumed to be mutually exclusive activities [33,35]. At first, a similar distinction appears to apply to plants. Plants have a search cost represented by the ability to locate the nutrient and grow roots nearby [14,20]. Handling costs might consist of nutrient uptake, processing of nutrients into forms suitable for transport and transport throughout the plant [23,27,28].

However, a closer look at plant physiology shows that the costs of search and handling are difficult to separate. For example, when a root is used to both search out and handle a nutrient, how does one score the cost of constructing and maintaining that root? Similarly, transpiration is an energetically expensive process in plants, driving the transport of solutes from roots to shoots in the xylem which could be considered handling costs [49,52]. However, transpiration also creates a gradient in soil water potential that influences movement of ions near the roots, which could be considered a search cost. Further complicating this issue, many plants produce exudates or form symbioses with microbes that enhance nutrient availability, soil exploration and nutrient capture, but at a significant energetic cost to the plant [53,54]. Thus, we suggest that foraging costs in plants should also be framed by some function, $f(c_{ij})$, which describes the combined sum of costs in units of energy or potential fitness lost through missed opportunities within root $i$ on ramet $j$. This sum need not include every biological process, but only those which are thought to be biologically relevant to the question at hand. Equation 3 now becomes

$$\frac{E_{Gained}}{E_{Spent}} = \sum_{i=1}^{n}\sum_{j=1}^{m}\frac{f(r_{ij})}{f(c_{ij})}. \qquad \text{[Equation 4]}$$

The function $f(c_{ij})$ is different from the term $(T_S + T_H)$ in Equations 1–3 because it can have more than two terms and the individual costs will be categorized into biological functions rather than as search or handling. A consequence of this adjustment is that Equation 4 suggests that foraging should maximize efficiency, whereas Equation 1 suggested that foraging should maximize a rate.

## Foraging plants should maximize absolute gains

A problem with efficiency expressed as a ratio is that it is difficult to distinguish between very large gains which come at very large costs and very small gains which come at very small costs [38]. A more basic problem with Equation 4 is that it is mathematically inappropriate to take a summation of a ratio. Because our framework allows the units of benefits and costs of plant foraging to be the same, we can rethink the structure of Equation 4. We propose that plants should be expected to maximize absolute energy or fitness gains across all foraging roots and ramets (i.e. benefits − costs):

$$E_{Gain} = \sum_{i=1}^{n}\sum_{j=1}^{m}\big(f(r_{ij}) - f(c_{ij})\big). \qquad \text{[Equation 5]}$$

Equation 5 is not mathematically derived from our previous equations. Instead, our five equations serve as signposts which reveal the logical development of our view of plant foraging. First, we acknowledged that foraging plants exhibit modular growth. Thus, plants should maximize the sum of all foraging units rather than the behaviour of each unit independently (Equation 2). Second, the benefits of plant foraging are complex and must be expressed by a function that describes both the potential benefits and interactions of the limiting nutrients of interest (Equation 3). Third, the costs of plant foraging cannot be easily demarcated into search or handling. Instead, the biologically relevant costs of plant foraging must be accounted for individually (Equation 4). Finally, it is more appropriate to expect plants to optimize absolute foraging gains than foraging efficiency (Equation 5).

## Five directions for research in plant foraging behaviour

Similar to animal models, Equation 5 is a simplification of reality. The strength of such frameworks comes from the explicit and quantitative predictions they support about the costs and benefits of foraging behaviours. It will take significant theoretical and empirical research to transform $f(r_{ij})$ and $f(c_{ij})$ to fully parameterized models of plant behaviour. Furthermore, the exact form of $f(r_{ij})$ and $f(c_{ij})$ will depend on the foraging questions to be addressed (Boxes 3,4). Ideally, Equation 5 will serve as a starting point for others to begin to think about how to use an optimization framework to explore plant foraging in novel ways. Below, we propose five areas for future research that such a framework suggests to us. These research directions do not necessarily require detailed parameterization of Equation 5, rather they are based on coarse manipulations of costs and benefits, and the measurement of easily observed ecologically meaningful responses such as plant performance (i.e. $E_{gain}$).

### *When a nutrient is available to a plant as multiple chemical species, what is the optimal 'diet' of these alternative chemical forms?*

This is a question of prey choice (Box 3), and has received some attention [55,56]. For example, nitrogen is available to plants in a variety of chemical forms, and there is interspecific variation in the growth responses to these different forms [55,56]. However, it is unclear why such variation exists and whether it follows any specific rules. Nonetheless, we can predict from Equation 5 that if the costs associated with using each chemical form vary among plant species, then plants should have differentially specialized 'diets' when a mixture of chemical forms is available.

### *When an environment consists of patches of variable quality, how much effort should plants expend in each patch?*

This is a question of patch use (Box 4), and has been extensively studied in plants [11–13]. Plants generally increase root growth in nutrient-rich patches relative to the surrounding background soil; however, there are exceptions [11–13]. An optimality model could provide insight into these exceptions, because plants should only proliferate into patches if the potential benefits outweigh the costs. This seems obvious, but has only rarely been quantitatively addressed [31,57]. Furthermore, Equation 5 can be modified to factor in distance among patches, or distance from the stem [35,39,58]. This would create a model of plant foraging which is more similar to the marginal value theorem (Box 4) [31,58].

### *What is the optimal strategy for energetic investment in the different foraging modules of a plant?*

Maximum plant fitness in Equation 5 is achieved when the summation of benefits minus costs is summed across all foraging units. However, Equation 5 does not specify how variable the individual contributions of each foraging unit should be. Identical optima could occur if a plant has an 'average' return from every foraging unit, or if it gains all of its return from a single foraging unit. The optimal behaviour will depend on how sensitive plants are to variance in resource availability [59,60]. Plants that invest in only a few high-gain foraging units might be considered risk prone, whereas plants that invest in many lower, but consistent-gain foraging units might be considered risk averse [59,60]. This idea of risk-sensitive behaviour is well documented in animal foragers.

### *Under what conditions would a plant increase investment in mutualists instead of increasing investment in its own roots?*

Mutualisms can represent a significant cost but also a significant benefit to plants [54,61]. However, not all plant species form mutualisms, and environmental context can also play a role in the degree of root mutualisms [54,61]. Optimality theory would suggest that if the cost of investing in new roots is less than the cost of forming a mutualism, then a non-mutualist response should be favoured. Similarly, if the potential benefits obtained from roots are potentially higher than those obtained from mutualists, a non-mutualist response should be favoured. Benefits and costs should ultimately interact to shape the degree of mutualism, and this should be predictable using an optimality framework.

### *Are plant root foraging decisions influenced by predation risk in different soil locations?*

Like mutualisms, predation also represents a significant potential foraging cost. A rich animal literature explores the effects of predators on foraging decisions in animals and identifies additional tradeoffs related to reproductive state and variance in food rewards [38,39,43]. This prediction is also supported by an optimality framework because herbivory can be considered a form of cost. Foraging in areas of high herbivory should only be favoured if the potential energetic gain outweighs the potential energetic losses associated with herbivory [62]. The evolutionary history of a plant with herbivores might also explain why some plants do not exhibit strong foraging responses.

## Conclusion

In this paper, we have presented a conceptual foundation that places plant root foraging within a larger subdiscipline of behavioural ecology. Our goal in this brief essay is to inspire others to begin to think more quantitatively about optimality in plant behaviour. We urge plant ecologists to approach the idea of plant behaviour from a more theoretical perspective that accounts for the assumption that behaviour is ultimately determined by the principle of optimality, and to exert more effort thinking at the level of the individual. To achieve this, we encourage plant behaviourists to tap into the large volumes of behavioural theory developed for animals, much of which can be applied (with modification) to plants (e.g. [2,31,48,58]). We have made five suggestions where we see research parallels between plant and animal foraging. We believe an optimality approach has the potential to significantly advance the broader study of both plant behaviour and eventually behavioural ecology as a whole.

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