

A modular concept of plant foraging behaviour: the interplay between local responses and systemic control

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ABSTRACT

In this paper we examined the notion that plant foraging for resources in heterogeneous environments must involve: (1) plasticity at the level of individual modules in reaction to localized environmental signals; and (2) the potential for modification of these responses either by the signals received from connected modules that may be exposed to different conditions, or by the signals reflecting the overall resource status of the plant. A conceptual model is presented to illustrate how plant foraging behaviour is achieved through these processes acting in concert, from the signal reception through signal transduction to morphological or physiological response. Evidence to support the concept is reviewed, using selective root placement under nutritionally heterogeneous conditions and elongation responses of stems and petioles to shade as examples. We discussed how the adoption of this model can promote understanding of the ecological significance of foraging behaviour. We also identified a need to widen the experimental repertoires of both molecular physiology and ecology in order to increase our insight into both the regulation and functioning of foraging responses, and their relationship with the patterns of environmental heterogeneity under which plants have evolved.

Key-words: environmental heterogeneity; plasticity; module; resource acquisition; roots; shade-avoidance response; signal transduction pathway; signals.

INTRODUCTION

In natural communities, the availability of resources can vary widely both in space and over time. For example, nutrient availability from the substrate can differ by as much as an order of magnitude between the locations occupied by different roots of a single plant (Jackson & Caldwell 1993; Gross, Pregitzer & Burton 1995; Farley & Fitter 1999). Patches of available nutrients are also ephemeral because they are quickly taken up by microbes or plant roots

(Hodge, Robinson & Fitter 2000). Another example are steep gradients in both the amount and spectral quality of light experienced by leaves from the top to the bottom of plant canopies and along forest edges or close to tall vegetation patches in a horizontal plane (Ballaré 2009). Even though monoculture stands may appear homogeneous, leaves may receive very different amounts of radiation (Tang & Washitani 1995) because shoots are clumped and leaf densities vary spatially in a fine-scaled pattern (van der Hoeven, de Kroon & During 1990). Temporal variation in light supply is considerable, both in forests (Chazdon & Pearcy 1991) and in dense stands of herbaceous vegetation (Percy, Roden & Gamon 1990) because of the periodic occurrence of sunflecks.

Given that plants have evolved under these extremely heterogeneous environmental conditions, ecological interest in plant foraging is primarily concerned with the implications of this form of behaviour for future resource acquisition and, ultimately, fitness. Following Hutchings & de Kroon (1994) we define foraging responses as the plastic physiological or morphological alterations that directly or indirectly enhance the capture of essential resources. Aboveground, such responses include the shade-induced elongation of stems and petioles by which laminae are projected upwards, along gradients of increasing photon flux density, into locations with higher light availability (e.g. Schmitt & Wulff 1993; Huber, Fijan & During 1998), and the light-fleck-induced activation of the photosynthetic apparatus that increases the capture of ephemeral light pulses (Percy 1990). Foraging responses belowground include the initiation and activation of lateral root primordia (Nibau, Gibbs & Coates 2008) and the subsequent growth of lateral roots in patches of substrate with high nutrient concentration, and also the activation of nitrate transporters in response to high nitrate availability (Okamoto, Vidmar & Glass 2003; Gan *et al.* 2005). Foraging behaviour is thus concerned with responses that enhance future resource uptake, rather than with growth processes that are modified as a result of this uptake (Hutchings & de Kroon 1994).

Plant foraging is one of the most important aspects of plant behaviour, and its manifestation is an expression of phenotypic plasticity (Silvertown & Gordon 1989; Hutchings & de Kroon 1994; Sultan 2000; Trewavas 2005). de Kroon *et al.* (2005) proposed that phenotypic plasticity is

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not a whole-plant phenomenon but that it is expressed at the level of the repeated, often semi-autonomous structural and functional subunits (modules) from which plants are constructed (White 1979; Preston & Ackerly 2004). To enable comparison of the foraging behaviours of roots and shoots, we consider modules to be the analogous 'resource-acquiring structures' that plants position selectively within their heterogeneous environments. For our purposes, therefore, aboveground modules are 'metamers' (White 1979) composed of a stem internode, a leaf and an axillary meristem. Belowground they are the young root axes, including the zones where elongation and lateral branching occur. In this conceptualization a plant consists of an interconnected network of modules, each with the ability to sense and respond to its environment (White 1979; Haukioja 1991; de Kroon *et al.* 2005; Fig. 1).

de Kroon *et al.* (2005) have further argued that phenotypic responses to the environment, such as those involving decisions about branching frequency, and the elongation of internodes and root axes, are made at the level of the module, and that the responses are induced by signals that are locally perceived. At the same time, these responses are modified by signals received from other connected modules that may be exposed to different conditions, resulting in an integrated and adaptive response at the level of the whole plant to its whole environmental context.

Here we argue that plasticity at the level of the individual module is an essential mechanism without which plant foraging behaviour cannot be accomplished. Only by varying significantly at very fine spatial and temporal scales can plant responses to external signals achieve the precision necessary to exploit locally detected nutrient patches, or to grow away from locally detected patches of shade. Because foraging responses act to optimize resource capture for all integrated modules, there must also be integrating controlling mechanisms that can override or modify local responses. In the first part of this paper, we present a conceptual model of modular foraging to illustrate how the pathway from signal to response integrates local and distant (systemic) cues. Next, for two well-defined foraging responses – selective root placement and the shade-avoidance response – we consider how much is currently known about the regulation of foraging behaviour through the interplay between local detection and response, and systemic modification of the response. Finally, we discuss how this regulatory model may assist in understanding the ecological significance of foraging behaviour. We have chosen to use the responses to nutrients and shade as examples because foraging for these resources has been well-studied, and because together they illustrate how our conceptual model might operate above- as well as belowground. We would argue that our concept applies equally well with respect to foraging for other resources such

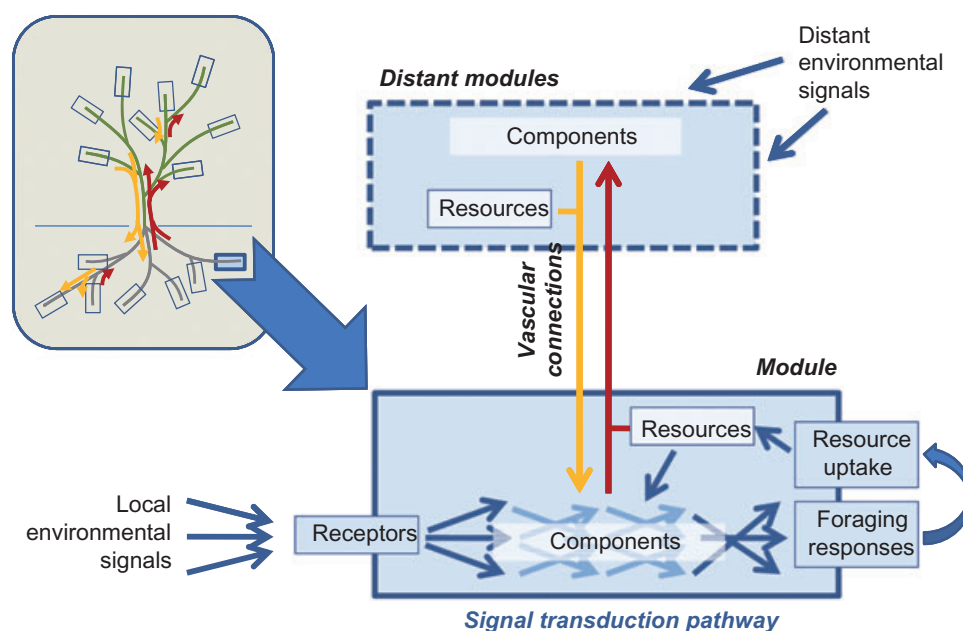


Figure 1. The inset depicts a plant consisting of below- and aboveground interconnected modules. Orange and red arrows are the up- and downstream vascular flows, functionally connecting modules both within the root system and within the shoot system, and between roots and shoots. Each module has receptors detecting the local environmental quality, triggering a cascade of events within the module (the signal transduction pathway), eventually leading to foraging responses. This signal transduction involves the sequential up- or downregulation of gene expression resulting in the production of signal transduction components, that is, mRNA and transcription factors including proteins, metabolites, hormones, etc. Foraging responses may feedback locally through local resource uptake, which may be sensed directly or via enhancing the internal resource levels within the module. Foraging responses also feedback globally through systemic signals received via the vascular connections, moderating the local responses. Resources and signal transduction components released in other parts of the plant and transported into the module may serve as systemic cues. Each module also exports components and resources into the vascular bundles contributing to the global cocktail of cues affecting the responses of distant modules.

as water or oxygen, as similar morphological and physiological alterations of root and shoot modules are involved in their acquisition (e.g. Voesenek *et al.* 2004; Wang, de Kroon & Smits 2007).

A MODULAR MODEL OF PLANT FORAGING

Like any other form of plasticity, any foraging response starts with a localized external signal (Fig. 1). The signal can be the abundance of the external resource itself (e.g. the number of photons in incident radiation) or a derivative of resource availability (e.g. the red to far-red ratio of light), as a measure of local environmental quality. The signal is perceived by specific receptors that bind to the signaling molecule and then adopt a different form. For example, absorption of red photons converts phytochrome from an inactive to an active form (Smith 2000). We expect that receptors will generally be located close to the site of the local response (e.g. regions of active cell division in stems and petioles at which elongation responses occur). For example, nitrate perception appears to be associated with two major nitrate receptors that are present close to the sites where new lateral roots may be initiated in response to localized patches of high nitrate concentration in the substrate (Guo *et al.* 2001; Linkohr *et al.* 2002; Wirth *et al.* 2007).

Receptor conversion elicits a cascade of genetic and biochemical responses in a signal transduction pathway (e.g. Voesenek *et al.* 2004; Vandenbussche *et al.* 2005; Nibau *et al.* 2008) in which genes are up- or downregulated, resulting in production or inhibition of regulatory proteins (such as transcription factors), and microRNAs. These, in turn, activate or block other genes, resulting in a complicated network consisting of multiple interacting paths, including changes in hormone concentrations and hormone sensitivity. We will refer to all the intermediary products in the pathway from signal to response as 'signal transduction components' (Fig. 1). The sequential changes of these signal transduction components ultimately lead to foraging responses.

The localized nature of signal perception and response allows for local feedback, which may be external from the environment. For example, foraging activity and resource capture lower the external resource concentration and reduces the strength of the external signal. Potentially, local foraging may also feedback internally, because resource acquisition improves the resource concentration within the module (Fig. 1). Resources (or their metabolic products such as sugars and amino acids) can be sensed internally (Smeekeens 2000; Forde 2002; Francis & Halford 2006; Lam *et al.* 2006), triggering a pathway that interacts with the signal transduction pathway as described earlier, affecting the concentration of, and/or sensitivity to, signal transduction components. Local feedbacks provide modules with the opportunity to tune their foraging efforts to the quality of the local environment.

Despite their localized and semi-autonomous nature, the foraging responses of modules are subject to modification

by cues from other interconnected modules (cf. Zhang *et al.* 1999; Berleth & Sachs 2001; Fig. 1). Typical systemic cues that are transported in the vascular bundles include resources and hormones (Trewavas 2005), and possibly other components of the signal-transduction pathway. These products are unloaded from the xylem and phloem and sensed within the module where they interact with the signal transduction pathway as it is expressed locally (Fig. 1). This interaction can lead to substantial modifications to local physiological or morphological responses (Hartnett & Bazzaz 1985; Hutchings & Price 1993; Stuefer, de Kroon & During 1996; Sachs & Novoplansky 1997). Straightforward predictions are that a local response to resource abundance will be enhanced when many other integrated modules are growing under conditions of resource shortage, and that this will result in elevated resource uptake at a local scale. Conversely, the local response will be reduced when foraging efforts are unlikely to improve an already favourable plant resource status (Lamb, Haag & Cahill 2004).

LOCAL AND SYSTEMIC SIGNALS INFLUENCING SELECTIVE ROOT PLACEMENT

The interplay between local and systemic cues is prominent in root foraging for nitrate. In several plant species, locally applied nitrate has been found to stimulate the number of developing laterals and their elongation (e.g. Drew, Saker & Ashley 1973; Sattelmacher *et al.* 1993; Robinson 1994). Experiments with *Arabidopsis thaliana* seedlings on vertical agar plates confirmed that a greater lateral root density was produced in nitrate-rich agar patches (supplied as narrow horizontal bands), because more lateral root primordia developed into lateral roots when primary roots grew through these patches in an otherwise nitrate-poor background substrate (Zhang & Forde 1998). In contrast, seedlings grown on *homogeneously* high nitrate substrate showed strong suppression of lateral root development (Zhang *et al.* 1999). This indicates that the same local conditions (high nitrate) can elicit entirely different local responses, depending on the resource status of the plant. Thus, systemic signals (in this example the plant's internal N concentration) may overrule the effect of the local signal-transduction pathway (Forde 2002).

Insight into the local perception of and regulation by external nitrate and its interaction with systemic control by internal N status has recently come from studies using *Arabidopsis* mutants (Forde & Walch-Liu 2009). Nitrate transporter proteins NRT1.1 and NRT2.1 have been proposed to act as nitrate receptors close to the location where new lateral roots may be induced (Little *et al.* 2005; Remans *et al.* 2006a). Mutants of NRT1.1 showed a strong decrease in lateral root formation in response to a nitrate patch (Remans *et al.* 2006a). Moreover, NRT1.1 appeared to act upstream of ANR1 (Remans *et al.* 2006a), a MADS-box transcription factor that is part of the signal transduction for this local nitrate response (Zhang & Forde 1998). For NRT2.1, the effect of locally available nitrate on lateral root

development has not been determined yet, although studies on mutants for NRT2.1 grown on homogeneous low nitrate have indicated a nitrate uptake-independent role of this protein in determining the number of lateral root primordia that are induced. This suggests that, like NRT1.1, NRT2.1 is an upstream component of nitrate sensing (Little *et al.* 2005; Remans *et al.* 2006b).

NRT1.1 and NRT2.1 are strongly and positively regulated by the external nitrate concentration around the roots (Okamoto *et al.* 2003). The plant's N status also affects the gene expression of at least one of the two transporter proteins. The existence of such a systemic signal was shown in split-root experiments, where deprivation of nitrogen in one part of the root system led to an increased NRT2.1 expression in the non-deprived part (Gansel *et al.* 2001).

Notwithstanding the examples given earlier, detailed split-root designs or other experiments in which nitrate has been applied only locally to the root system are still scarce in studies on the regulation of resource uptake and root morphology. This prevents firm conclusions being drawn about the respective functions of local versus systemic signalling, even though circumstantial evidence point to additionally controlling mechanisms apart from the local signalling. For instance, apart from its regulation by NRT1.1, ANR1 expression also changes when external nitrate concentrations change, but data on this process seem at first sight inconsistent. Compared with N-depleted roots, high nitrate provided on an agar plate up-regulated *ANR1* gene activity in very young seedlings (Zhang & Forde 1998), whereas homogeneous high nitrate in a nutrient solution supplied to roots of more well-developed plants suppressed it (Wang *et al.* 2000; Gan *et al.* 2005). However, these contrasting results may suggest that ANR1 regulation as a component of the pathway towards nitrate-induced lateral root production is also controlled by a systemic (potentially shoot-borne) signal depending on the plant developmental stage or maybe N status of the shoot. It is unlikely that ANR1 is the only transcription factor that interacts with N signalling in the roots, as the expression of at least nine other root-transcribed MADS-box transcription factors responded to the nitrate treatment of *Arabidopsis* roots (Gan *et al.* 2005). This suggests the existence of a network of regulating factors that modulate the responses of individual roots to N supply.

The systemic signals that supply local roots with information about the N status of the plant are still unknown, although the amino acids that are formed during N metabolism may be strong candidates for this role. These N metabolites can be sensed even at very low concentrations, as has been shown in studies of the GLR proteins, which probably have a function as glutamate receptors in *Arabidopsis* (Forde & Lea 2007). Other compounds that are transported through the vascular system, such as small peptides, microRNAs, carbohydrates and hormones, may also play a role in the monitoring of N status within, and subsequent signalling between, plant modules (Forde 2002).

Studies on the regulation of selective root placement in which phosphate has been applied locally are probably

even more scarce than similar studies on the effects of nitrate. Linkohr *et al.* (2002) showed that *Arabidopsis* plants respond strongly to localized phosphate availability when grown on vertical agar plates, confirming earlier work (e.g. Drew 1975). Other studies on the signal transduction of phosphate-induced responses have been limited to applying either homogeneous high or low phosphate concentrations. In contrast to N signalling, however, a shoot-derived signal has recently been identified that is involved in phosphate-signalling (Grennan 2008). A group of microRNAs (miR399s) are induced by low phosphate concentration in the shoot (Chiou *et al.* 2006), and then move through the vascular bundles into the root, where they enhance phosphate uptake and translocation (Lin *et al.* 2008; Pant *et al.* 2008). Although miR399s are the first systemic signals that have been shown to regulate P uptake, it is likely that other long-distance signals play a role as well, together with signals that indicate the local phosphate conditions, as has been suggested by Lin *et al.* (2008). These recent studies provide ample opportunities to study local versus systemic signalling in plants growing in conditions where foraging is needed. It will be intriguing to discover which of the signal transduction components mentioned earlier are involved in the responses of roots to localized phosphate-rich patches.

LOCAL AND SYSTEMIC SIGNALS INFLUENCING SHADE-AVOIDANCE RESPONSE

Current information on the regulation of shade-avoidance responses (reviewed by Bou-Torrent, Roig-Villanova & Martinez-Garcia 2008; Franklin 2008; Ballaré 2009) shows that the local perception-transduction pathways of light within individual modules are interwoven with systemic signals that arise from a crosstalk between light and hormones (Morelli & Ruberti 2002). The local fine-tuning of the responses is achieved by the utilization and coordinated action of several photoreceptor families specialized for perception of different wavelengths in the incident radiation (Casal 2000; Chen, Chory & Fankhauser 2004; Vandembussche *et al.* 2005) with phytochrome B (phyB) playing a central role in the regulation of foraging responses to light (Ballaré 2009). In recent years, increasing attention has been paid to the analysis of the effects of plant hormones, such as ethylene, auxins and gibberellins, on the expression of shade-induced plasticity (Pierik *et al.* 2004; Vandembussche *et al.* 2005; Djakovic-Petrovic *et al.* 2007).

Shading is detected at a localized, modular level, that is, single-stem internodes or petioles. The local regulation pathways depend on whether plants are subjected to brief or prolonged shade from surrounding vegetation (Franklin 2008). Immediately after the onset of shading, phyB is converted from the far-red absorbing form (Pfr) to the red absorbing form (Pr). This FR-induced conversion results in increased stability of the PHYTOCHROME-INTERACTING FACTORS (PIFs), followed by the increased degradation of the growth-repressing DELLA proteins, which inhibit cell elongation. This removes an important constraint for cell elongation that is needed for

initial fast elongation responses in hypocotyls, although in petioles, the action of additional factors appears to be needed to initiate elongation (Djakovic-Petrovic *et al.* 2007). Over the longer term, the increased abundance of PIF4 increases gibberellin synthesis. Increased GA concentration again leads to increased degradation of DELLA proteins, thereby promoting increased PIF function. This loop promotes stem and petiole elongation (Franklin 2008).

Induction of elongation by a low R : FR ratio in the incident light also requires the presence of auxin. Auxin, which is produced predominantly in the young leaves of the shoot tip, and transported in a polar direction to the root tip, is a typical long-distance signal. Polar auxin transport is affected by light climate (Morelli & Ruberti 2002). In the absence of shade, auxin is primarily transported through the central core of the shoot, but under shaded conditions it may be transported in the outer layers of cells. The latter transport route is less efficient, and it involves increased auxin concentrations in the outer cell layers and the leaves, and lower concentrations in the central part of the shoots and in the root system, thereby affecting the lateral auxin gradient. This alteration in the lateral auxin gradient in shaded shoots results in reduced cell expansion in the leaves and increased cell elongation in the stem. As auxin is the only hormone that shows polarity of transport within the vascular tissue, it has been suggested that it acts as a systemic mechanism coordinating plant growth (Berleth & Sachs 2001; Morelli & Ruberti 2002), but it is also systemically controlling shade-avoidance responses that ultimately take place at the local, modular scale.

In addition to hormones, whole plant sugar concentration can be an important factor in the modulation of growth responses. However, sugars have a dual function, as they act both as resources and/or as signals that influence many physiological and developmental processes in plants (Smeekens 2000; Moore *et al.* 2003). An intermediate concentration of sucrose has been shown to promote the growth of petioles, irrespective of the light conditions (Kozuka *et al.* 2005). Shade-induced elongation responses follow an optimum curve, with the greatest elongation occurring under intermediate shade and relatively little elongation, or even shortening of stems and stem analogues, taking place under deep shade. This may be explained by balancing of the investment of the total carbon pool between the conflicting demands of increasing carbon assimilation, storage and growth (Smith & Stitt 2007). If the carbon concentrations are too low, investment of carbon into increased elongation may lead to further decrease of the carbon concentration and have deleterious effects on metabolic processes that are necessary for plant survival. Carbohydrate sensing and signalling mechanisms may thus enable plants to act appropriately in response to changing environmental conditions (Smith & Stitt 2007), thereby acting as systemic signals that operate by integrating whole plant resource status. It would be interesting to study the expression of local plastic responses in modules subjected to different availabilities of light as a function of the total

resource status of the plant. Such work would reveal whether reduced elongation under very low light intensity is primarily controlled by a shortage of carbon for growth, or whether it has evolved as a direct response to local light availability.

Despite strong systemic control by hormones and whole plant sugar levels, fine-tuning of shade-avoidance responses to local conditions is still possible. Boonman *et al.* (2007) recently showed that photosynthetic capacity, which is partially regulated by the concentration of cytokinins, can vary at a local, modular scale. Cytokinins are produced in the roots and transported via the xylem to the leaves. Under shade, transpiration decreases, which leads to a decrease in the cytokinin import to the leaves and to reduced photosynthetic capacity. External application of cytokinins to the leaves rescues the photosynthetic capacity to some extent (Boonman *et al.* 2007). This study elegantly shows how interaction between systemic and local cues leads to fine tuning of plant responses to the local environmental conditions.

Further experiments, in which parts of larger plants with a more complex modular structure are shaded and localized gene expression analysed, will allow local and distant cues to be distinguished. Such work is likely to provide new information about essential regulatory components involved in shade-avoidance responses and to promote a better understanding of the localization of light signal perception and its effects on photomorphogenesis (Bou-Torrent *et al.* 2008).

ECOLOGICAL SIGNIFICANCE OF THE MODULAR CONCEPT OF FORAGING BEHAVIOUR

Current information on the regulation of foraging behaviour, as summarized earlier, provides ample evidence that plants have evolved a system of local signal perception and response, modified by systemic signals from more distant modules. This regulatory system provides adaptive adjustment to the fine-scaled variation in resource availability in the environments of plants. However, we probably know even less about the ecological and evolutionary consequences of foraging behaviour than we do about its regulation (Karban 2008). How can the knowledge of the interplay between local processes and their systemic modification help us to understand the consequences of foraging for plant growth and reproduction?

In a meta-analysis of the root foraging responses of over 100 species, Kembel & Cahill (2005) found that the strength of response was extremely variable and that the benefits in terms of whole plant growth in heterogeneous versus homogeneous conditions was not related to the precision of root placement (Fig. 2). There is evidence to suggest that much of this variation in foraging response is caused by the uncontrolled variation in plant resource status affecting the local response through systemic signals. This can be seen in the negative correlation between the selectivity of root placement in nutrient-rich patches and the duration of experiments (Kembel & Cahill 2005). The larger size that

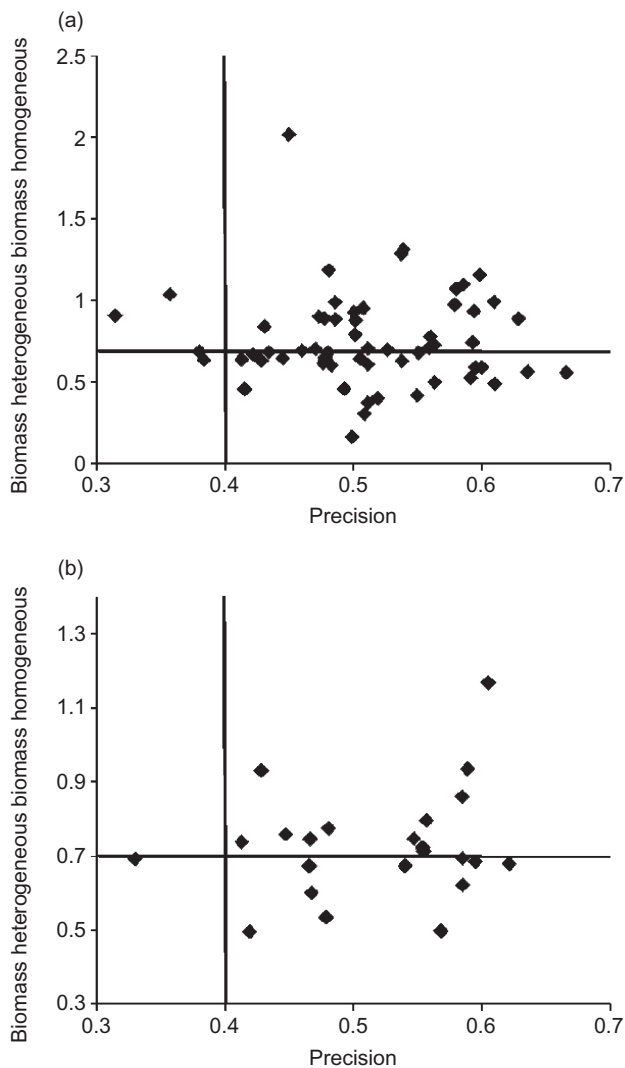


Figure 2. Relationships (data points represent species) between root foraging precision (i.e. the amount of roots in nutrient rich patches compared with the amount of roots in a similar volume of nutrient-poor background soil) and growth response to nutrient heterogeneity (plant biomass in heterogeneous soil/biomass in homogeneous soil) for two data sets. The amount of roots was measured as root surface area [(a) Great Plains flora data set] or root biomass [(b) combined biomass data set]. All data were $\ln(x + 1)$ transformed. The vertical line indicates where root densities are the same in rich and poor patches, showing that most species place more of their roots in the rich patches, but that the degree of selectivity of root placement is extremely variable between species. The horizontal line indicates where there is no difference in growth between plants in the homogeneous and heterogeneous treatments. Correlations between foraging precision and plant growth response were not significant ($P > 0.05$; phylogenetically independent contrasts), indicating that species with a larger proportion of roots in rich patches do not gain more in terms of greater growth. Modified from Kembel & Cahill (2005). Reproduced with permission of the University of Chicago Press.

plants can achieve in longer experiments also allows the accumulation of more nutrient reserves that can have a stronger negative feedback on foraging responses than in young seedlings and shorter experiments. For example, Jansen *et al.* (2006) showed with *Rumex palustris* that nutrient reserves that had been accumulated during early growth were redistributed within the plant at a later stage, satisfying part of the nutrient demand of the larger plant and lowering the necessity to forage as efficiently as earlier in its life. At this later stage of growth, precise matching between root placement and nutrient availability has little influence on plant growth (Jansen *et al.* 2006). These results corroborate other accounts (Hutchings & John 2004; Kembel & Cahill 2005; de Kroon & Mommer 2006; Hutchings & Wijesinghe 2008), suggesting that much of the variation in root foraging response seen between the experiments can be explained by the variation in the systemic signals influenced by the size and resource acquisition history of the plants under study, and the duration of experiments.

As with root foraging, the expression of shade-avoidance responses also depends on the systemic signals providing information about whole plant resource status, as discussed earlier. Other systemic triggers also play a role in shade avoidance, induced by factors such as day length (Salter, Franklin & Whitelam 2003), mechanical stress (Anten *et al.* 2009) and conditions experienced at earlier life history stages (Weinig & Delph 2001), which are usually perceived at the level of the whole plant rather than at the individual modules. These interactive effects of different environmental cues can be interpreted as mechanisms enabling plants to optimize their acquisition of light through elongation responses. For example, the moderating effect of mechanical stress on the elongation response in shaded plants prevents them from exceeding a critical height at which they become structurally unstable and vulnerable to bending and breaking (Anten *et al.* 2009).

Despite the prominence of systemic signals in shade avoidance, the responses of modules can be surprisingly localized if plants are subjected to heterogeneous conditions, with even adjacent connected modules expressing contrasting phenotypes. For example, especially in experiments on clonal plants, it has been shown that petiole elongation and the outgrowth of meristems at stolon nodes respond strongly to locally perceived conditions (Novoplansky, Cohen & Sachs 1990; Turkington, Sackville Hamilton & Gliddon 1991; Thompson 1993; Dong 1995; Hay *et al.* 2001; de Kroon *et al.* 2005). As yet, we have little understanding of the way in which local detection and response is apparently able to overrule systemic signals, or of the way in which these localized shade-avoidance responses affect whole plant fitness.

If the foraging process consists essentially of local processes of detection and response, with systemic signals modifying these processes, its investigation requires experimental designs in which the local and systemic effects can be clearly separated. However, in many of the current experimental designs for the study of foraging, the effects of these processes are confounded. Lack of evidence of

selective root placement under heterogeneous conditions, for example (Kembel & Cahill 2005; Fig. 2), may thus be because of the contrast between the patches being low (Wijesinghe & Hutchings 1999), or the systemic effects causing potentially strong local responses to be moderated by signals from connected modules in contrasting conditions, or by the signals reflecting whole plant resource status. Differences in foraging responses between species (Kembel & Cahill 2005) or between different genotypes within species (Walch-Liu *et al.* 2006; Walch-Liu & Forde 2008) may arise from the differences in the capacity for local detection and response and/or from differences in the way in which systemic signals affect these responses. In order to increase our understanding of the way in which foraging behaviour differs between species, we must widen our experimental repertoire so that local processes and systemic influences can be more clearly distinguished.

CONCLUSIONS

We have proposed a conceptual model in which plant foraging behaviour operates at the level of the repetitive units (modules) from which plants are constructed, with local responses modified by systemic signals that provide information on the conditions in which connected modules find themselves, and whole plant resource status (Zhang *et al.* 1999; Berleth & Sachs 2001). We have reviewed evidence that supports this model.

Molecular physiologists have developed an extremely powerful investigative toolbox in the recent years, including techniques with the ability to pinpoint exactly when and where within the plant signals are perceived, and when signal transduction components are up- or down-regulated. Studies in which specific promoters modify gene expression locally within the plant, and the use of reporters such as GFP, which can visualize where signal transduction components are being formed, are particularly useful techniques to expose aspects of the foraging process at a local level. Recent work using grafts between plants with different genetic make-up may provide additional information about the existence and mode of action of systemic signals (Bainbridge *et al.* 2005; Lin *et al.* 2008). Use of this molecular toolbox over the coming years can be expected to significantly increase our understanding of the regulation of plant foraging behaviour.

If the interplay between local responses and systemic modifications of the response is an essential feature of plant foraging, we should subject our experimental plants to the heterogeneous conditions in which this regulatory system has evolved. However, with some notable exceptions (Zhang & Forde 1998; Remans *et al.* 2006a; Boonman *et al.* 2007), contemporary studies on the molecular and physiological mechanisms of foraging responses have rarely examined the effects of heterogeneous conditions on plants. Apart from their ecological relevance, heterogeneous treatments allow gene expression patterns and signal transduction components to be compared between modules that are similar in developmental status. This approach also allows

assessment of systemic signals in heterogeneous environments in which control over the resource status of the whole plant is likely to be particularly critical. In contrast, ecological studies have a long tradition of subjecting plants to heterogeneous conditions and analysing the significance of foraging characteristics for plant performance. However, as we have argued, currently used experimental designs often fail to control for the possibility of plant resource status influencing the systemic feedback on the foraging responses, and therefore do not allow for a clear separation of local and systemic influences on plant performance. Acceptance of a modular concept of plant foraging behaviour therefore calls for a widening of the experimental repertoires of both molecular physiology and ecology, to improve our understanding of regulation and functioning of foraging responses in relation to the patterns of environmental heterogeneity under which plant species have evolved.

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