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The nutritional control of root development

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Abstract

Root development is remarkably sensitive to variations in the supply and distribution of inorganic nutrients in the soil. Here we review examples of the ways in which nutrients such as N, P, K and Fe can affect developmental processes such as root branching, root hair production, root diameter, root growth angle, nodulation and proteoid root formation. The nutrient supply can affect root development either directly, as a result of changes in the external concentration of the nutrient, or indirectly through changes in the internal nutrient status of the plant. The direct pathway results in developmental responses that are localized to the part of the root exposed to the nutrient supply; the indirect pathway produces systemic responses and seems to depend on long-distance signals arising in the shoot. We propose the term 'trophomorphogenesis' to describe the changes in plant morphology that arise from variations in the availability or distribution of nutrients in the environment. We discuss what is currently known about the mechanisms of external and internal nutrient sensing, the possible nature of the long-distance signals and the role of hormones in the trophomorphogenic response.

Abbreviations: ABA, abscisic acid; NR, nitrate reductase; P_i, inorganic phosphate

Introduction

> *The difficulty lies not in the new ideas, but in escaping the old ones.*
>
> *John Maynard Keynes.*

A characteristic feature of plant development is that it does not follow a rigidly predefined plan but instead is continuously susceptible to modification by interactions with the environment. A major function of this plasticity is to enable plants to overcome some of the constraints of their sessile lifestyle and to explore their surroundings for essential resources such as light, water and nutrients. Above ground, variations in light intensity and quality elicit photomorphogenic responses such as changes in internode and petiole length and in leaf area and thickness (Grime et al., 1986). In ecological terms, these responses provide a means by which plants can forage for light in competition with their neighbours. Below ground, there is equally strong competition for edaphic resources (water and nutrients). As with light, the supply of these is variable in both space and time and can frequently limit growth. It is therefore not surprising that root development, like shoot development, is highly plastic and that roots too manifest a foraging response when presented with localized supplies of nutrients (Robinson, 1994).

While rapid progress is being made in elucidating the phytochrome-mediated signal transduction pathways that convert light signals into morphological responses (Ballaré, 1999; von Arnim, 1999), much less attention has been paid to how nutritional signals are perceived and transduced in plants. Here we will first review the variety of ways in which nutrient supply affects root development and then go on to discuss the relative contributions of localized and systemic regulatory mechanisms. The remainder of the review will examine how far we have got in understanding the molecular basis for nutritional control of root development.

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Developmental processes in the root influenced by nutrient supply

It is appropriate at this point to insert some notes of caution. In considering the examples of nutritional modification of root development described here, it should be appreciated that in many cases data are available only for a small number of plant species. One thing that is clear about developmental plasticity is that different species (and even different genotypes within a species) can and often do respond differently to the same environmental stimulus. These differences in response are usually quantitative, but there is at least one example where the same nutritional stimulus elicits the opposite response in two genotypes of the same species (Bonser et al., 1996). Thus although many of the responses discussed here have been selected because they are well-documented and have been observed in more than one species, it may not be safe to extrapolate to untested species or genotypes. It is also undoubtedly the case that the responsiveness of a plant to a particular nutritional stimulus is likely to be influenced by interactions with other environmental variables, so that the experimental conditions could well have a strong influence on the observed responses.

Another aspect of plant biology which could sometimes complicate the assessment of nutritional effects on plant development is the phenomenon of 'ontogenetic drift', whereby many phenotypic traits change dramatically during the course of plant growth and development (Coleman et al., 1994; Evans, 1972). For this reason, if a nutrient treatment affects the rate of growth and development (and is being applied for long enough to do so significantly) then it may not be meaningful to compare the morphology of plants of the same chronological age. In such cases it may be necessary to use plant size or developmental stage as the basis for comparisons (Coleman et al., 1994; Evans, 1972). This can be particularly relevant in the case of the shoot:root ratio, which in some herbaceous plants increases markedly over the first few weeks of growth (Bazzaz et al., 1989). While ontogenetic drift is unlikely to be a major factor in any of the other morphogenetic effects discussed below, it will always be important to keep the phenomenon in mind when assessing any apparent examples of phenotypic plasticity in plants.

Root growth and branching

One of the most commonly observed effects of nutrient deficiency on plant development is a decrease in the shoot:root ratio, particularly in fast-growing species adapted to sites of high fertility (Chapin, 1980). Deficiencies in N, P or S all result in a shift in dry matter allocation in favour of root growth (Ericsson, 1995). However, simple measurement of the relative biomass of the shoot and root fails to reveal the many subtleties of the roots' response to changes in nutrient supply. For example, while K deficiency does not affect the shoot:root ratio in barley (*Hordeum vulgare*) (Drew, 1975) it does cause marked changes in root architecture by inhibiting lateral root growth without affecting seminal root growth or the numbers of primary lateral roots (Hackett, 1967).

Nearly 140 years ago it was reported that plants growing on concentrated nutrient solutions developed a short, compact and densely branched root system, while on dilute solutions or water the roots were long, thin and more sparsely branched (Nobbe, 1862). This general response to variations in the nutrient supply has since been reported many times in a wide range of species (reviewed by Wiersum, 1958). In his studies, Wiersum noted that nutrient deficiency (particularly NO_3^- deficiency) produced faster-growing taproots and diminished root branching in several dicot species. In barley, deficiencies in N, P or K all led to a marked decrease in the lengths of both first- and second-order lateral roots, while seminal root length was unaffected (Drew, 1975). A similar response to P deficiency was noted in maize (*Zea mays*) (Mollier and Pellerin, 1999). Note that it seems to be a general rule in plants that primary root growth is much less sensitive to nutritional effects than is the growth of secondary or higher-order roots

The positive effect of nutrients on root branching becomes most apparent when the nutrient supply is localized in the soil. On encountering a soil patch that is rich in nutrients (particularly N or P), the roots of many plant species respond with an increased rate of root growth and branching that is localized to the nutrient-rich patch (Robinson, 1994). This response enables the plant to optimize its allocation of resources by concentrating its root growth within the region of the soil that will yield the most benefit in terms of nutrient capture. It has been shown to be of particular ecological importance in situations where neighbouring plants are competing for limited resources (Hodge et al., 1999; Robinson et al., 1999).

The first detailed experiments describing the plant's responses to localized supplies of individual macronutrients were performed on barley by Drew and his colleagues (Drew, 1975; Drew and Saker, 1975, 1978; Drew et al., 1973). These demonstrated the spectacular way in which NO_3^-, NH_4^+ or P_i (inorganic phosphate), when applied to one segment of a seminal root, stimulated lateral root proliferation specifically within that segment. The increased root proliferation was the result of increased numbers of both primary and secondary lateral roots and a significant stimulation of the elongation rate of the lateral roots in the zone of treatment. Of the nutrients tested, only K failed to elicit a response, and studies on other species have confirmed the absence of localized proliferation in K-rich patches (Robinson, 1994). Why there should be this difference between K and other macronutrients is unclear.

Recent studies with Arabidopsis showed that a localized supply of NO_3^- stimulated lateral root elongation by 2- to 3-fold in the NO_3^--rich zone and that even 0.1 mm NO_3^- (when the rest of the root received 0.01 mm) was sufficient to elicit the maximal response (Zhang et al., 1999). Unlike barley, but similar to maize (Sattelmacher and Thoms, 1995), the localized NO_3^- supply had no significant effect on lateral root initiation.

Intriguingly, a recent report suggests that it is not only macronutrients that are able to trigger a localized branching response. When one-half of a split-root system of the Zn hyperaccumulator species *Thlaspi caerulescens* was exposed to soil enriched for Zn (at 250–1000 mg kg^{-1} soil), that portion of the root system showed increased biomass and length (Whiting et al., 2000). These experiments showed that hyperaccumulator species have the ability to forage for metals at concentrations that are inhibitory to root growth in non-accumulator species from the same genus. This unexpected observation raises the question whether the ability to perceive and respond to heavy metals (and perhaps other micronutrients) is widespread amongst plants. In non-accumulator or metal intolerant species the response would only be detectable at a much lower range of heavy metal concentrations because of the inhibitory effects of metal toxicity on root growth.

Although lateral roots may respond to localized supplies of a nutrient in a localized fashion, this response is not necessarily completely autonomous because the intensity of the response can also be affected by the nutrient supply to the rest of the root system. Thus, for example, an external supply of 1 mM NO_3^- stimulated lateral root growth more strongly in barley when the remainder of the root system was in low NO_3^- than if it too was in high NO_3^- (Drew et al., 1973). Similarly, roots of P-stressed bean plants presented with a P-enriched soil patch branched more intensively within the patch than did roots of unstressed plants (Snapp et al., 1995).

Root diameter

Fine roots allow the root system to explore the soil volume effectively while minimizing the investment needed to construct and maintain the root system. Thicker roots are more costly to produce, but have greater transport capacity and are less vulnerable to desiccation, physical damage, pathogens and grazing by soil-borne microarthropods and so are generally longer-lived (Fitter, 1987). Many plant species accommodate this trade-off by exhibiting plasticity in root diameter according to the environmental conditions. The fineness of a root is often expressed as specific root length (length per unit weight of root) and roots with high specific root lengths (i.e., fine roots) are often found in plants grown under nutrient deficient conditions (Fitter, 1985).

Changes in the overall fineness of a root system as a result of changes in nutrient supply can sometimes be attributed to changes in the relative proportions of different orders of root. Thus if increased branching results from an increase in the nutrient supply, the result will be an increase in the average specific root length of the root system (Bilbrough and Caldwell, 1995; Fitter, 1976; Robinson and Rorison, 1983). However, in some cases the nutrient supply can also have a direct effect on the specific root length of individual roots. For example, first order lateral roots of wheat (*Triticum aestivum*) growing in a NO_3^--rich patch were significantly thicker than similar roots growing in the absence of NO_3^- (Hackett, 1972). Similarly in barley, a high concentration of NO_3^- was associated with a doubling in the diameter of both first- and second-order laterals, but there was no effect on the diameter of the seminal axis (Drew et al., 1973).

Root diameter generally shows less plasticity than stem diameter, and in many species specific root length does not change significantly as a function of nutrient availability (Hutchings and de Kroon, 1994). In a comparison of a fast-growing species (*Dactylis glomerata*) and a slow-growing species (*Brachypodium pinnatum*) that co-occur in many nutrient-poor calcareous grasslands, it was found that only the former developed thicker roots when grown under conditions of high N or P (Ryser et al., 1997).

Few studies have examined the cytological basis of the plasticity in specific root length. However, Drew et al. (1978) observed that the increased diameter of lateral roots in their localized NO_3^- treatment was due to a 2-fold increase in the diameter of the stele and in the numbers of cells in both the stele and cortex.

Root angle

An important factor in determining the distribution of the root system in the soil is the angle of growth of the roots. There are intrinsic differences between the gravitropic response of different root types within a single root system: for example secondary roots tend grow out from their parent root at an angle, allowing them to escape the nutrient depletion zone and explore the soil volume more effectively. In addition, recent studies have found that some roots display a marked plasticity in their response to gravity. This was revealed by studies in which several legume species were supplied with a range of phosphate concentrations (Bonser et al., 1996; Liao et al., this vol). Under conditions of low P availability the growth angle of the basal roots (the roots that emerge laterally from the base of the hypocotyl) was reduced (i.e., they became more horizontal) compared to roots adequately supplied with P. This nutritional response was observed in bean (*Phaseolus vulgaris*), soybean (*Glycine max*) and pea (*Pisum sativum*). Other mineral deficiencies (N, K, S, Ca or Mg) had no effect on root angle.

A survey of 16 different bean genotypes revealed considerable variation in their responsiveness to P stress: six showed a reduced growth angle, nine failed to respond and one responded with an increased growth angle (Bonser et al., 1996). Since P availability is normally highest near the soil surface, the production of a shallower root system under P stress is likely to be an important contributor to the efficiency of P acquisition (Ge et al., 2000). In agreement with this, a bean genotype with high efficiency of P capture under field conditions had basal roots that were much more responsive to P stress than did a P-inefficient genotype (Liao and Yan, 2000).

Root hair length and density

Root hairs are tubular outgrowths on the root surface that play an important role in increasing the root's ability to capture nutrients. Not only do root hairs increase the absorptive capacity of the root by greatly increasing its surface area, they also serve to expand the nutrient depletion zone around the root. The latter is particularly important for access to relatively immobile nutrients (such as P) and can make a significant contribution to the efficiency of nutrient uptake (Gahoonia and Nielsen, 1997). Root hairs have uptake systems for most if not all macro- and micronutrients (including Pi, K^+, NH_4^+, NO_3^-, Cl^- and Zn^{2+}) (Gilroy and Jones, 2000).

Both the density of root hairs on the root surface and their length are known to be highly sensitive to a range of environmental factors, including the supply of certain nutrients (Gilroy and Jones, 2000). Root hair production responds particularly strongly to P deficiency: when rape, spinach and tomato plants were grown at P_i concentrations >100 μM, root hairs were infrequent and short, whereas at low P_i (<10 μM) they were long and abundant (Foehse and Jungk, 1983). Similar effects have been reported in Arabidopsis seedlings grown in culture on high and low P_i (Bates and Lynch, 1996).

In many plant species, Fe deficiency also has a marked stimulatory effect on root hair production (Schmidt, 1999). This response is seen in dicots and in non-grass monocot species as part of a series of physiological and developmental adaptations that help to mobilise Fe in the soil (known as strategy I). Roots of the Poaceae (grasses) use a different strategy involving the secretion of phytosiderophores and subsequent uptake of the Fe(III)–phytosiderophore complex (strategy II) (Schmidt, 1999). Fe deficiency substantially increased both the length and number of root hairs in *Arabidopsis*, the response being seen within 24 h of transferring the seedlings to –Fe medium (Moog et al., 1995).

Perhaps surprisingly, it is not only low mobility nutrients that affect root hair development. There are many reports that root hair development is also negatively affected by the NO_3^- supply (Boot and Mensink, 1990; Foehse and Jungk, 1983; Kohls and Baker, 1989; Robinson and Rorison, 1987; Thornton, 1936). In spinach (*Spinacea oleracea*), root hair length was 7-fold higher at 0.01 mM NO_3^- compared to 1 mM (Foehse and Jungk, 1983). Foehse and Jungk did not report the effect of NO_3^- on root hair density, but other studies have shown negative effects on root hair numbers in oil-seed rape (Bhat et al., 1979), alfalfa (*Medicago sativa*) (Thornton, 1936) and *Casuarina cunninghamiana* (Kohls and Baker, 1989).

There seems to be much greater species-to-species variability in root hair responsiveness to NO_3^- than to P, with some species such as tomato (Foehse and Jungk, 1983) and some grasses (Robinson and Rorison, 1987) failing to show any response to NO_3^- under the conditions tested.

Root hairs develop from a subset of root epidermal cells termed trichoblasts. The first step in root hair development is the specification of cell fate, when an epidermal cell becomes a trichoblast and destined to produce a root hair. A number of Arabidopsis genes (e.g., *TTG* and *GL2*) have been identified as important regulators of this first step (Gilroy and Jones, 2000). Subsequent developmental stages include root hair initiation (when a bulge begins to form in the trichoblast cell wall), tip elongation and finally root hair maturation. The observations that root hair length and root hair density can be affected independently by nutrient stress are consistent with genetic evidence that initiation and growth of root hairs are under separate genetic control (Gilroy and Jones, 2000; Schiefelbein et al., 1993).

Relatively little work has been done to establish which of the first two stages of root hair development (cell fate determination or root hair initiation) is sensitive to the nutrient supply to account for the observed effects on root hair density. In the case of Fe there is evidence that it may be trichoblast specification which is modulated. Under conditions of nutrient sufficiency, trichoblasts develop exclusively over the anticlinal walls between underlying adjacent cortical cells (Gilroy and Jones, 2000). In Fe-deficient plants, root hairs form ectopically (i.e., over periclinal cortical cell walls) (Schmidt et al., 2000), indicating that cells which would otherwise be atrichoblasts are being triggered to develop as trichoblasts. This contrasts with the effect of water stress in *Arabidopsis*, where a drought-induced absence of root hairs was reported to result from a block in the second step (initiation) and not in trichoblast specification (Couot-Gastelier and Vartanian, 1995).

Root hair length is determined both by the rate and by the duration of tip growth. In P-deficient Arabidopsis plants, both components of growth contributed to the increased length: the maximum rate elongation under low P was 67% higher than under high P and the duration of growth was increased from 5.5 to 8.25 h (Bates and Lynch, 1996). Thus at least three separate stages of root hair development in *Arabidopsis* are susceptible to regulation by the P supply. It will be of great interest to discover, by means of genetic approaches, whether there is one common regulatory mechanism for all three stages or whether separate pathways operate.

Nodulation

The development of N-fixing nodules on legume roots is a highly regulated process. The number of nodules on a root system is controlled by a mechanism called 'autoregulation', in which previously formed or forming nodules suppress the development of further nodules (Schultze and Kondorosi, 1998). Split-root experiments have established that autoregulation acts systemically and that the autoregulatory signal originates in the shoot (Kosslak and Bohlool, 1984). However in addition to autoregulation, or perhaps superimposed upon it, is a strongly suppressive effect of combined N (especially NO_3^-) which legumes will utilise as a N source in preference to forming the N-fixing symbiosis (Carroll and Mathews, 1990). Nitrate inhibition of nodulation has been one of the clearest and most intensively studied examples of the nutritional control of plant development. Unlike other factors that inhibit nodulation (such as pH, temperature or toxicity), NO_3^-does so in a very specific way without interfering with plant growth (Carroll and Mathews, 1990). However, the sensitivity of nodulation to NO_3^- is strongly dependent on the plant species and genotype (Carroll and Mathews, 1990).

Nitrate is reported to block or delay the nodulation process at a number of different stages, including both rhizobial infection (by inhibiting root hair curling and infection thread formation) and nodule development, as well as inhibiting nitrogenase activity in established nodules and triggering early nodule senescence (Carroll and Mathews, 1990). Studies on soybean have shown that if the NO_3^- treatment is delayed until 18 h after rhizobial inoculation its inhibitory effect is greatly diminished (Malik et al., 1987), indicating that in this species the earliest stages of nodulation are the most sensitive. In experiments with vetch (*Vicia sativa*) it was shown that to be effective at suppressing root hair deformation an NH_4NO_3 treatment had to begin at least 24 h before the addition of the rhizobial Nod factor (which is able to initiate the process of root hair curling) (Heidstra et al., 1994). The finding that the root hairs had to develop in the presence of NH_4NO_3 for its effect to be seen, suggested that the NH_4NO_3 treatment might be interfering with perception or transduction of the Nod factor signal or that that the NH_4NO_3 somehow alters the development of the root hairs so that they are unable to curl (Heidstra et al., 1994). The former possibility was eliminated when the NH_4NO_3 treatment was shown not to block induction by the Nod factor of the *VsLb1* gene, which is one of the earliest events in the root hair's response to rhizobial infection (Heidstra et al., 1997).

Cluster roots

Roots of some plant species adapted for growth on nutrient-poor soils are able to develop unusual bottlebrush-like structures consisting of discrete root segments flanked by densely packed clusters of short lateral roots (rootlets) (Skene, 2000; Skene, this volume). Often called proteoid roots because of their association with the family Proteaceae, cluster roots have also been reported in half a dozen other families of plants, including the Leguminoseae (Watt and Evans, 1999). A cluster root is distinct from a normal root in that the numerous rootlets are closely packed, develop only within distinct segments of the parent root (0.5 – 1 cm long) and all grow to a similar length. The rootlets are determinate and when they reach their final length the meristem is lost and root hairs develop all the way to the tip. Like normal lateral roots, the rootlets initiate from the pericycle. Cluster roots not only massively increase the surface area of the root for little additional investment in root biomass (in a similar way to root hairs), they also help to mobilize P and Fe by exuding high concentrations of organic acids (mainly citrate) into the rhizosphere.

Cluster roots are usually associated with P- or Fe-deficient soils, and both the numbers of cluster roots and their structure (rootlet length and density) are variable according to the extent of deficiency (Watt and Evans, 1999). Although one legume species (*Lupinus consentinii*) will form cluster roots under either Fe or P deficiency, it is more usual that plants responsive to Fe deficiency are not responsive to P deficiency and vice versa (Watt and Evans, 1999). Some species (e.g., white lupin, *L. albus*) are less sensitive to the presence of P in the soil and will produce some cluster roots even at P levels found in fertile agricultural soils (Keerthisinghe et al., 1998). When the ability of other nutrient stresses to stimulate cluster root formation in white lupin was tested, it was found that a –Mn treatment had a small stimulatory effect, while –N, –K and –Fe had none (Johnson et al., 1994).

Distinguishing between external and internal nutritional signals

There appear to be at least two ways by which plants monitor their nutrient supply: directly through localized changes in nutrient concentration in the external soil solution, or indirectly through changes in the internal nutrient status of the plant itself (Fig. 1). The direct pathway has the advantage that it can allow the plant to respond to short-term changes in nutrient availability and can in effect provide the roots with spatial information about the distribution of nutrients within the soil profile, allowing it to concentrate its developmental responses to that region of the soil where they will be of most benefit for nutrient acquisition. The indirect pathway has the advantage that it enables the plant to integrate its nutritional signals with those coming from range of other physiological processes (such as photosynthesis). In this section we will consider on a case-by-case basis the evidence for the existence of each of these regulatory pathways.

Root growth and branching

The localized proliferation of roots within nutrient-rich soil patches is the clearest and best-documented example of a developmental response to an external nutrient supply. As discussed above, this response consists of an increased rate of lateral root elongation, sometimes accompanied by stimulation of lateral root initiation, specifically in regions of the root in contact with the enriched nutrient source (usually N or P). However, it is evident that root branching is also under some form of systemic control, i.e., it is not only dependent on the prevailing external nutrient concentration but also on the nutrient status of the plant as a whole. This is seen for example in the experiments of Drew et al. (1973), where the number of first-order lateral roots in the middle section of the barley root was markedly reduced if the top and bottom sections were supplied with 1 mM NO_3^- rather than 0.01 mM NO_3^-. Similarly, split root experiments with Douglas fir (*Pseudotsuga menziesii*) seedlings showed that when the plants were N-stressed (by depriving the major part of the root of N) the extent of root branching in the N-rich zone was enhanced twofold compared to unstressed plants (Friend et al., 1990).

Recent experiments with *Arabidopsis* have thrown light on one possible mechanism by which the internal N status of the plant may modulate root branching (Zhang and Forde, 1998; Zhang et al., 1999). Roots

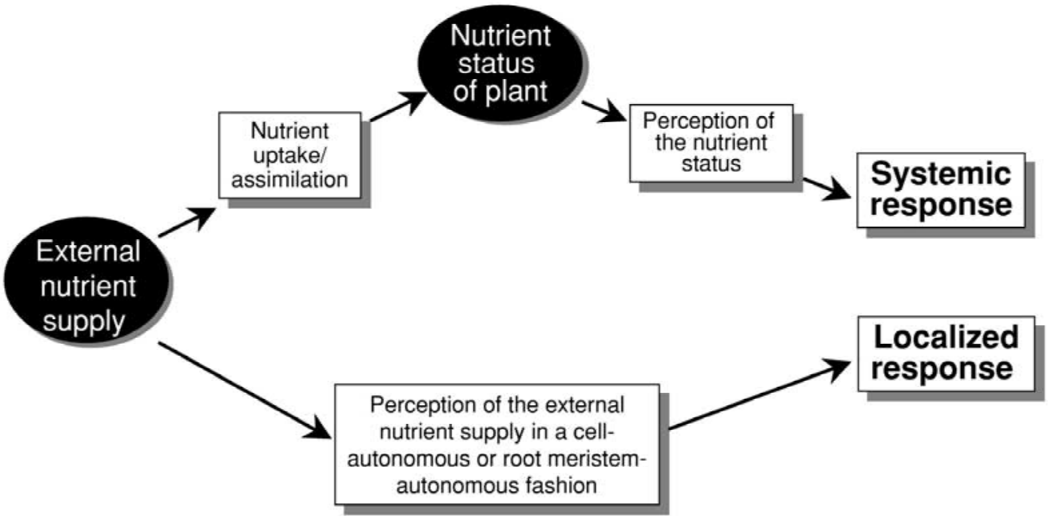

Figure 1. Alternative pathways for nutritional control of plant development.

of *Arabidopsis* seedlings growing on agar plates were uniformly supplied with a range of KNO_3 concentrations (0.01 – 50 mM) and the effects on root growth and branching analysed. Concentrations in the range 1 – 50 mM had no significant effect on elongation of either primary roots or mature lateral roots. However, these high NO_3^- concentrations led to a marked reduction in the number of visible lateral roots. Detailed microscopic examination of the early stages of lateral root development at 1 – 50 mM NO_3^- revealed that the high rates of NO_3^- supply were having no effect on lateral root initiation itself, but rather were causing a pronounced delay in lateral root development at around the time of emergence from the parent root. The result was the appearance of stunted lateral roots <0.5 mM in length. The numbers of stunted lateral roots increased progressively as the NO_3^- concentration was increased above 1 mM, so that by 50 mM (a concentration higher than would normally be found in soils) almost 100% were stunted.

If the lateral roots were allowed to progress up to or beyond the point of emergence before the plants received the 50 mM NO_3^- treatment, there was no effect on their growth (Zhang et al., 1999), demonstrating that there is a very specific stage of lateral root development which is sensitive to the high rate of NO_3^- supply. These stunted lateral roots were only temporarily blocked: if the experiment was extended for a further 7 days or so many of them had matured and were elongating at normal rates. This effect of NO_3^- appears to be a systemic rather than a localized one: when the 50 mM NO_3^- was applied locally to just one part of the primary root it had a much smaller inhibitory effect than when it was applied to the whole root system, and this inhibitory effect was not restricted to the zone of treatment (Zhang et al., 1999).

The effect of high rates of NO_3^- supply on lateral root development seems to be related to the internal NO_3^- pool. This is indicated by the finding that a nitrate reductase (NR) deficient mutant (*nia1nia2*) was more sensitive than the wild-type to the presence of high external concentrations of NO_3^-, i.e., the mutant produced a higher proportion of stunted lateral roots at a given NO_3^- concentration (Zhang et al., 1999). There may be analogies here with experiments previously done with low NR lines of tobacco: accumulation of NO_3^- in the shoots of these lines leads to much higher shoot:root ratios than in N-sufficient wild-type plants, even though the low NR lines are severely deficient in organic N (Scheible et al., 1997b). As in *Arabidopsis*, the effect appeared to be mainly due to a decrease in the numbers of lateral roots (Stitt and Feil, 1999), but unfortunately it was not established whether lateral root initiation or some later stage of lateral root development was affected in the tobacco plants. Split root experiments had previously established that the inhibition of root growth due to NO_3^- accumulation in the low NR lines was systemic and therefore likely to involve a shoot-derived signal (Scheible et al., 1997a).

It therefore appears that NO_3^- regulates root branching in both a localized and a systemic manner: its external presence stimulates the elongation of those mature lateral roots in direct contact with it (and in some cases lateral root initiation as well), while its accumulation inside the plant to concentrations above a certain threshold leads to a reduction in the numbers of mature lateral roots. This general pattern of response seems to apply to a wide range of species (from *Arabidopsis* to Douglas fir), although whether the details are always the same as in *Arabidopsis* remains to be established.

Root diameter

Localized signals may be responsible for modulating root diameter. When wheat or barley roots were subjected to a localized treatment with NO_3^-, the lateral roots growing in the NO_3^--rich zone were significantly thicker than those not exposed to NO_3^- (Drew et al., 1973; Hackett, 1972). It has been noted that there is a positive correlation between root diameter and root elongation rate (Cahn et al., 1989; Thaler and Pages, 1996), so that the changes in root diameter observed in the NO_3^--rich zone could be causally linked to the localized stimulation of lateral root elongation. There may be other regulatory mechanisms affecting the specific root length independently of growth rate, and perhaps these could operate systemically.

Root angle

Split-root experiments with bean showed that the decreased growth angle of the basal roots is a systemic response to low P: both 'low P' and 'high P' roots in a split-root system had growth angles similar to those in high P only (Bonser et al., 1996).

Root hairs

Again using split roots, evidence has been obtained that root hair growth is correlated not with the P or NO_3^- concentration outside the roots but rather with the internal P or N status of the plant (Foehse and Jungk, 1983). The additional finding that an alternative source of N (in the form of NH_4^+) did not affect root hair formation might suggest that internal NO_3^- pools were more relevant to root hair growth than the pools of other N metabolites (Foehse and Jungk, 1983).

In a developmental study with *Arabidopsis* seedlings it was found that the differences between root hair length in 'low P' and 'high P' plants did not show up until 6 days after germination, after which the newly developed root hairs became progressively longer in the 'low P' plants and progressively shorter in the 'high P' plants (Bates and Lynch, 1996). This would again seem to be most consistent with an effect of the internal P content of the seedlings rather than the external P concentration. However, the same study provided contradictory evidence that was more consistent with a localized effect of the external P concentration: when the tip of a 'low P' root was treated with a high P_i concentration it inhibited root hair growth specifically within the 'high P' zone, while the reverse experiment (treating the tip of a 'high P' root with low P_i) stimulated it. Perhaps both systemic and localized pathways contribute to the regulation of root hair growth in *Arabidopsis*.

Nodulation

Wilson (1917) reported that nodule formation in soybean was inhibited only in those parts of the root directly exposed to the NO_3^- supply. The conclusion that the inhibition of nodulation is primarily a localized response to NO_3^- has since been confirmed in a number of different studies (for review, see Carroll and Mathews, 1990). Nevertheless, some systemic effect of NO_3^- on nodulation has not been completely ruled out. When the NO_3^- concentration supplied to the NO_3^--fed half of the split-root system is sufficiently high, nodule development in the NO_3^--free half can be inhibited (Carroll and Gresshoff, 1983; Hinson, 1975). Other evidence for systemic effects of NO_3^- came from experiments in which NO_3^- was supplied either above or below the site of inoculation and was still effective in inhibiting nodulation (Malik et al., 1987). Since there is genetic evidence for a relationship between autoregulation of nodulation (a systemic phenomenon) and NO_3^- inhibition of nodulation (Day et al., 1989), it may be that NO_3^- interacts with the autoregulatory process at more than one level, accounting for both localized and systemic effects (see below).

Cluster roots

There is only a limited amount of information about the relative contribution of localized and systemic signals in regulating cluster root formation. Cluster roots tend to be most abundant in parts of the soil richest in organic matter (Watt and Evans, 1999), but this could be due to the higher water content of such patches rather than localized nutrient supplies per se. On the other hand, proteoid root formation in white lupin and *M. cerifera* was suppressed by foliar application of

P (Dinkelaker et al., 1995), suggesting the importance of the P status of the plant and a likely role for systemic signals in modulating cluster root formation. This conclusion is supported by a recent study in which phosphonate (HPO_3^{2-}) was used as a tool to investigate the role of internal P status in regulating proteoid root development (Gilbert et al., 2000). Phosphonate is an analogue of inorganic phosphate that is reported to interfere with plant perception of internal P concentration (Carswell et al., 1997). Treatment of P-sufficient white lupin plants with phosphonate led to a dramatic increase in the number cluster roots, and the induced rootlets displayed the full repertoire of physiological changes associated with proteoid root development (Gilbert et al., 2000). Unfortunately, progress in elucidating the molecular mechanisms involved in regulating cluster root formation is being hampered by the lack of suitable well-characterized genotypes and mutants of the relevant species.

Mechanisms

In this section we review our state of knowledge about the mechanisms by which nutrients can exert both localized and systemic effects on developmental processes in roots.

Localized responses

The fact that many of the ions that are able to stimulate localized developmental responses in the root are highly mobile within the plant (Marschner, 1995) would argue against a simple 'first-come first-served' model whereby the cells or roots in the immediate vicinity of the nutrient patch benefit most from its presence. On the other hand, the apparent hydraulic isolation of the root apex from the rest of the root due to lack of maturity of the xylem within the apical zone (Melcior and Steudle, 1993), could mean that the meristematic zone is dependent to at least some degree on external ions, providing a possible explanation for localized stimulation of root growth. However, a model of this kind would make it difficult to account for why the stimulatory effect is specific to certain ions (see above) and why it acts on lateral roots but not on primary roots.

Another explanation for localized lateral root proliferation was prompted by the observation that localized supplies of various nutrients (including NO_3^- and P) are associated with increased respiration rates in maize roots exposed to the nutrient patch (Sattelmacher and Thoms, 1995). It was proposed that the increased metabolic activity at the site of nutrient uptake creates a stronger sink for photosynthate from the shoot, and that the enhanced phloem unloading brings with it an influx of phytohormones (such as auxin) which promote root growth. However, an immediate difficulty with this model is the finding that a localized K^+ supply also stimulates respiration but does not affect root growth (Sattelmacher and Thoms, 1995).

In recent years we have begun to develop a greater appreciation of the remarkable sophistication of the nutrient sensing mechanisms available to both prokaryotic and eukaryotic cells. Bacteria use members of the family of two-component regulators to sense changes in their environment. For example the *Escherichia coli narX* and *narQ* genes encode transmembrane histidine kinases which act as external NO_3^- receptors and, in the presence of external NO_3^- or NO_2^-, activate transcription factors encoded by the *narL* and *narP* genes respectively (Merrick and Edwards, 1995). In budding yeast (*Saccharomyces cerevisiae*), transmembrane sensors for glucose, amino acids and NH_4^+ have been identified and found to be homologous to membrane proteins that act as transporters for the respective nutrients (Klasson et al., 1999; Lorenz and Heitman, 1998; Ozcan et al., 1996).

Although no analogous nutrient sensors have so far been identified in plants, there is good reason to believe that they do exist. An external supply of NO_3^- is able to trigger the rapid induction of a number of genes including those for NR, nitrite reductase and NO_3^- transporters. It has been shown that NR activity is not required for the induction to occur, clearly implicating the NO_3^- ion as the signal molecule (Deng et al., 1989; Pouteau et al., 1989). A number of lines of evidence suggest that the external presence of even very low NO_3^- concentrations (<10 μM) can be sensed by plant roots (reviewed in Forde and Clarkson, 1999). Using NR-deficient mutants it has been shown that NO_3^- stimulation of lateral root elongation in *Arabidopsis* (Zhang and Forde, 1998) and localized NO_3^- inhibition of nodulation in legumes (Carroll and Gresshoff, 1986; Jacobsen, 1984) are both independent of NO_3^- assimilation. In the former case the key role of the NO_3^- ion was confirmed by the finding that localized supplies of other N sources (NH_4^+ and glutamine) could not substitute for NO_3^- (Zhang et al., 1999).

With this background it seems not unreasonable to propose that the localized developmental responses to

NO_3^- (and probably to other nutrient ions as well) are also mediated via specific sensors or receptors on the plasma membrane (or elsewhere) and their associated signal transduction pathways. This would predict the existence of nutritionally regulated transcription factors or other regulatory proteins that could modulate developmental processes in response to changes in the external nutrient supply. A candidate for just such a protein was recently identified in the form of a root-specific and NO_3^--inducible member of the MADS-box family of transcription factors which is encoded in *Arabidopsis* by the *ANR1* gene (Zhang and Forde, 1998). Other members of the MADS-box family in plants are key regulators of floral organogenesis (Shore and Sharrocks, 1995) and evidence was obtained using antisense and co-suppressed lines that the *ANR1* gene is required for NO_3^- stimulation of lateral root elongation (Zhang and Forde, 1998).

A second *Arabidopsis* gene (*AXR4*) has also been implicated in the signalling mechanism linking external NO_3^- to increased rates of lateral root elongation. *AXR4* was originally identified in a screen for mutants in which root growth was less sensitive to auxin (Hobbie and Estelle, 1995). Root gravitropism is defective in the *axr4* mutants, but otherwise they display few of the pleiotropic effects associated with other auxin-resistant mutants. When several auxin-resistant mutants were tested for the ability of their lateral roots to respond to localized NO_3^- supplies, only *axr4* was found to be significantly defective (Zhang et al., 1999). This suggests that there is an overlap between the signal transduction pathways for auxin and NO_3^- signalling, but unfortunately the nature of the *AXR4* gene product is as yet unknown. A recent model for the signal transduction pathway linking external NO_3^- to increased rates of cell production in the lateral root tip is shown in Fig. 2.

There are some parallels between NO_3^- stimulation of lateral root growth and NO_3^- inhibition of nodulation. As discussed above, NO_3^- inhibition of nodulation is also (at least partly) a localized effect, and evidence from the use of NR-deficient mutants of pea and soybean indicates that here too the NO_3^- ion itself is able elicits the response (Carroll and Gresshoff, 1986; Jacobsen, 1984).

Mutants of both pea and soybean have been isolated which are NO_3^--tolerant for nodulation (Carroll et al., 1985; Postma et al., 1988) and these have helped to shed some light on the mechanism of NO_3^- inhibition. All NO_3^--tolerant mutants isolated so far are defective in the autoregulatory mechanism (and so also display a 'supernodulating' phenotype), and grafting experiments have shown that in most cases the mutant phenotype is controlled by the shoot (Carroll and Mathews, 1990; Delves et al., 1987; Francisco and Akao, 1993). This suggests that NO_3^- inhibition of nodulation acts through an interaction with the autoregulatory mechanism, which is thought to depend on the production of a phloem-mobile inhibitory signal (of unknown nature) in the shoot (Carroll and Mathews, 1990). A model has been proposed in which external NO_3^- acts by potentiating the effects of this autoregulatory signal in those parts of the root directly exposed to the NO_3^- (Gresshoff et al., 1988).

Intriguingly all the NO_3^--tolerant nodulation mutants also have an altered root phenotype (increased numbers of lateral roots and an increased shoot:root ratio), even when uninoculated with rhizobium (Day et al., 1986; Postma et al., 1988). In this respect the NO_3^--tolerant mutants have a constitutive 'high N' phenotype. It is therefore possible that the regulatory mechanisms responsible for autoregulation and NO_3^- regulation of nodulation have evolved from pre-existing mechanisms for regulation of root development and shoot:root partitioning that may be common to non-legumes. In this regard it is interesting that an alfalfa gene (*NMHC5*) which belongs to the same subfamily of MADS-box genes as *ANR1* (the *AGL17* subfamily) is expressed specifically in nodules (Heard et al., 1997). The function of the *NMHC5* gene product is so far unknown.

Another gene with a potential role in N regulation of nodulation has recently been identified in *Lotus japonicus* (Schauser et al., 1999). This gene (*Nin*), which is required for the formation of infection threads and the initiation of nodule primordia, encodes a putative transcription factor with homology to the Mid protein in *Chlamydomonas*. Mid is a developmental regulator involved in determining mating type during gametogenesis (Ferris and Goodenough, 1997), and since gametogenesis in *Chlamydomonas* is induced by N limitation it has been postulated that Nin might play a role in N regulation of nodulation(Schauser et al., 1999). Recently it was shown that NO_3^- inhibited gametogenesis and the expression of two gamete-specific genes even in NR-deficient mutants of *Chlamydomonas*, indicating that the NO_3^- ion itself is providing the negative regulatory signal for the sexual differentiation of the alga (Pozuelo et al., 2000). Thus Mid in *Chlamydomonas* and Nin in *L. japonicus* might be components of related signal transduction pathways that link the external NO_3^-

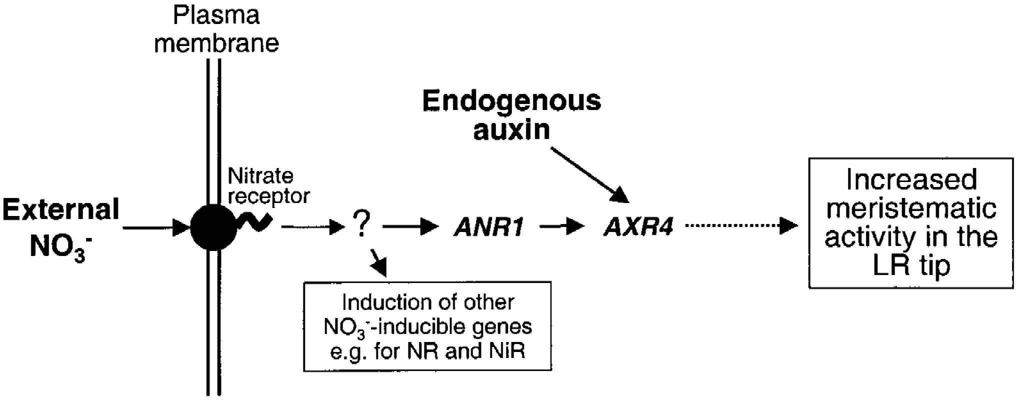

Figure 2. Model for the signalling pathway for NO_3^-regulation of lateral root growth. The question mark refers to the as yet uncharacterised part of the signalling pathway responsible for NO_3^- induction of gene expression. Diagram modified from Zhang et al. (1999). See text for further details.

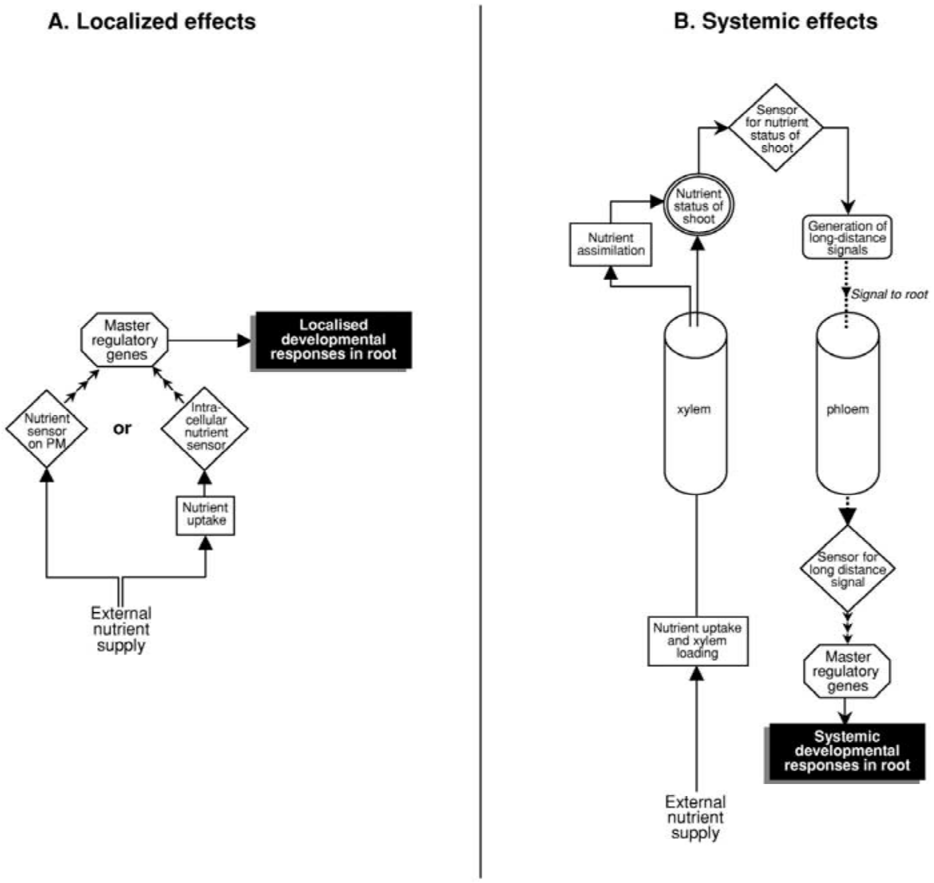

Figure 3. Generalised models for signalling pathways involved in (A) the localized and (B) the systemic responses to the nutrient supply. The existence of master regulatory genes that modulate the relevant developmental processes is proposed. These would also be subject to modulation by any other environmental signals to which those developmental processes were susceptible, and would therefore serve to integrate the plant's responses to multiple inputs.

supply to the negative regulation of two very different developmental pathways.

A generalized model for how an external nutrient supply may exert localized effects on developmental processes in roots is presented in Fig. 3A. Although it seems most likely that the external nutrient concentration is monitored directly by means of sensors or receptors in the plasma membrane of root epidermal or cortical cells (Forde and Clarkson, 1999), it is difficult to rule out the possibility that there are sensors inside these cells which are able to detect fluctuations in intracellular nutrient concentrations that occur in parallel with changes in the external supply.

Systemic responses

Where the root's response to the nutrient supply is systemic it appears that sensing of the plant's nutrient status takes place in the shoot and that the shoot is then the source of long-distance signals that regulate both physiological and developmental processes in the root. This raises a series of questions that as yet have few clear answers. How, at the molecular level, is the nutrient status of the shoot monitored? What key ions or metabolites are being monitored? What is the nature of the shoot-to-root signals? How are these signals perceived in the root? The fact that many nutritional responses are specific to particular nutrients indicates that the plant is able to monitor many different nutrients independently and to transmit nutrient-specific regulatory signals to the root.

Much of the effort to date in elucidating the mechanism of shoot-to-root signalling of nutrient status has been based on the physiological responses rather than the developmental ones. For example, the evidence that the uptake of inorganic ions by roots is regulated in accordance with the shoot's demand for the ions (Marschner, 1995), has led to a search for the means by which the shoot can communicate its requirements to the transport systems of the root. For N, it has been proposed that the rapid cycling of amino acids which occurs between shoot and root would serve to provide the root with the necessary information about changes in the shoot's N status (Cooper and Clarkson, 1989; Imsande and Touraine, 1994). However, contrary to the requirements of this model it is sometimes found that N deficiency can lead to an increase rather than a decline in amino acid cycling (e.g., Peuke et al., 1994). Furthermore, two detailed split-root studies on oil-seed rape and mung bean (*Ricinus communis*) confirmed that rates of NO_3^- uptake were strongly correlated with the shoot N content, but found no correlation with either the amino acid content of the root (Lainé et al., 1995; Tillard et al., 1998) nor with quantitative or qualitative changes in the amino acid content of the phloem (Tillard et al., 1998). Thus although it is possible that transient changes in phloem amino acid content could be missed, amino acid cycling seems unlikely to provide the shoot-derived signal that regulates either NO_3^-uptake or root development. In agreement with this, the decreased root growth found in NR-deficient tobacco lines is actually accompanied by an *increase* in the amino acid content of the roots (Scheible et al., 1997b). As yet there is no alternative candidate for the N signal.

The cloning of a gene encoding a chloroplast homologue of the bacterial P_{II} protein has provided a possible candidate for a component of the N sensing machinery in *Arabidopsis* shoots (Hseih et al., 1998). In *E. coli* and other bacteria, P_{II} (GlnB) is part of the regulatory pathway that controls transcription of a number of N assimilatory genes in response to cellular N status (Merrick and Edwards, 1995). However, the Arabidopsis P_{II}-like protein is localized within the chloroplast, and there may well be separate and distinct N regulatory pathways of a eukaryotic type which operate in the cytosol.

There is even less information about the mechanisms for monitoring and responding to the internal supplies of other nutrients. The *pho1* mutant of *Arabidopsis*, which is defective in P_i transport to the shoot, has been used to demonstrate that P-regulated genes in the root are responding not to Pi levels in the root but to the P status of the shoot (Bariola et al., 1994; Burleigh and Harrison, 1999). Whether the signal from the shoot is Pi itself arriving in the phloem or some other metabolite or signal molecule has yet to be established.

There is good evidence that Fe-deficiency responses in the root are controlled at least in part by shoot-derived signals (Schmidt, 1999), and it appears that the signal coming from the shoot is not Fe itself. The latter conclusion was based on grafting experiments using an Fe over-accumulating mutant (*dgl*) of pea which indicated that the *dgl* shoot was constitutively producing a signal compound of an unknown kind that was acting to stimulate Fe(III) reductase activity in the root (Grusak and Pezeshgi, 1996). A role for the non-protein amino acid nicotianamine (an efficient chelator of Fe(II) and Fe(III)) in sensing of internal Fe status has been hypothesized based on the Fe-overaccumulating phenotype of a nicotianamine-deficient tomato mutant (*chloronerva*) (Scholz et al., 1992). In addition, the root system of the recessive tomato mutant *fer* is unable to induce any of the characteristic responses to Fe deficiency (Bienfait, 1988; Ling et al., 1996) and the *Fer* gene product is thought to be a component of the Fe sensing or regulatory system responsible for induction of genes that mediate the Fe-deficiency responses (for a more detailed discussion of Fe sensing in plants and other organisms see Schmidt, 1999)

Fig. 3B shows a generalized model for systemic regulation of developmental processes in the root by means of long distance signals from the shoot.

Integrating localized and systemic responses

An important question is how the systemic and localized signals discussed above are integrated within the plant to produce the observed developmental responses. One way of integrating the different signals would be if the master regulatory genes depicted in Fig. 3A, B were the same, so that the localized and systemic signalling pathways converge. Something of this kind has been postulated for NO_3^- regulation of nodulation (Gresshoff et al., 1988), where a localized NO_3^- signal is proposed to interact with the systemic autoregulatory signal emanating from the shoot (see above). Cross-talk or convergence between different signal transduction pathways is becoming a well-established mechanism in plants by which signals from independent stimuli are integrated at the biochemical and genetic levels (Genoud and Métraux, 1999).

It is also possible for the systemic and localized signals to act on different stages of the developmental process, so that integration may only be achieved at the whole plant level. An example is seen in the effects of NO_3^- on root branching in *Arabidopsis* (Zhang et al., 1999). As discussed in detail above, it appears that the stimulatory effect of a localized NO_3^- acts mainly on elongation of mature lateral roots, while the systemic inhibitory effect of high NO_3^- status acts specifically on immature, emerging lateral roots.

Alternatives to nutrients and their metabolites as long-distance signals

The above survey would argue against a direct role for nutrients or their metabolites in communicating information to the root about the shoot's nutrient status. An alternative hypothesis would be that the shoot has mechanisms for monitoring the supply of certain key ions or metabolites, and then for modulating the production of phloem-mobile signal(s) that are perceived in the root and converted into appropriate metabolic and developmental responses (see Fig. 3B). What might those phloem-mobile signals be? Auxin is synthesized in the shoot and carried in the phloem, but given the specificity of the root's responses to changes in the supply of particular nutrients it is difficult to envisage how auxin on its own (or any of the other 'conventional' plant hormones) could confer that specificity.

In recent years it has become clear that the phloem carries a number of different classes of macromolecules (proteins and RNAs) which are potentially capable of transmitting long distance signals within the plant (Citovsky and Zambryski, 2000; Thompson and Schulz, 1999). A well-characterized example of a phloem-mobile peptide signal is systemin, a peptide involved in triggering systemic acquired resistance to pathogens, which is synthesized within the infected leaf and moved around the plant via the phloem (Ryan, 2000). A model has been proposed in which the nutrient and water status of the shoot is communicated to the root by means of proteinaceous signal molecules (Lucas, 1997). Evidence that a specific population of mRNA molecules circulate throughout the plant via the phloem has been obtained from studies on pumpkin (*Cucurbita maxim*) (Ruiz-Medrano et al., 1999). One particular species of mRNA (CmNACP), which is selectively translocated in the phloem, belongs to the 'NAC domain' gene family, some of whose members are involved in controlling apical meristem development. The hypothesis was therefore put forward that the phloem may act as an 'information superhighway', carrying signals in the form of phloem sap-specific mRNAs (or their encoded proteins) to enable developmental events in the various meristems of the plant to be integrated with physiological processes in the leaves (Ruiz-Medrano et al., 1999). These findings open up exciting new possibilities for how the shoot might be able to communicate its nutritional requirements to the root in highly specific ways.

Role of hormones in the response to nutrient supply

It is frequently observed that the plant's responses to changes in nutrient supply can be mimicked by exogenously applying a particular plant hormone. The conclusion then tends to be drawn that the hormone in question must play an important role in mediating the nutritional effects. For example, auxin and ethylene have been linked to the Fe-deficiency response (Schmidt, 1999), abscisic acid (ABA) and ethylene have been implicated in the response to P stress (Lynch and Brown, 1997; Trull et al., 1997), a role for ethylene in NO_3^- suppression of nodulation has been proposed (Ligero et al., 1999) and auxin transported from the shoot is reported to play a role in stimulating the formation of proteoid roots in P-deficient white lupin plants (Gilbert et al., 2000).

However, the evidence in favour of a role for a particular hormone in these nutritional responses is frequently circumstantial, and in a number of important cases the contrary evidence is quite compelling. When two ABA mutants (*aba1* and *abi2*) of *Arabidopsis* were analyzed for their developmental and physiological responses to P stress, they were found to be normal in most respects, implying that ABA does not have a major role in coordinating the P stress response (Trull et al., 1997). Schmidt et al. (2000) looked at the induction of Fe-deficiency symptoms (root hairs and ferric reductase activity) in 40 hormone-related mutants of *Arabidopsis*, including lines which were insensitive or resistant to auxin, cytokinin, ABA and ethylene. Both root hair formation and ferric reductase activity were enhanced by Fe-deficiency in all the mutants tested, making it difficult to argue a primary role for any of these hormones in the response. Furthermore, it was noted that the root hair response to applying the ethylene precursor ACC (1-aminocyclopropane-1-carboxylic acid) was qualitatively quite different from the root hair response to Fe-deficiency (Schmidt et al., 2000). The role of ethylene in NO_3^- suppression of nodulation is controversial. Several lines of evidence support a model in which NO_3^- acts by stimulating the production of ethylene, which then inhibits nodulation (Ligero et al., 1991, 1999). However, other workers have failed to confirm that ethylene inhibits nodulation in soybean (Hunter, 1993; Lee and La Rue, 1992), and experiments with ethylene-insensitive mutants of soybean found that they were equally sensitive to NO_3^- suppression of nodule numbers as the wild-type (Schmidt et al., 1999).

Since hormones such as auxin, cytokinin, ABA and ethylene play such an important part in all aspects of plant development and physiology, it would be surprising if they did not interact in some way with the nutritional effects discussed in this review. However, the evidence that nutrients modulate development by effecting changes in the levels of endogenous hormones is far from convincing. Nevertheless, it is becoming increasingly evident that signal transduction in plants involves extensive cross-talk between different signalling pathways (Genoud and Métraux, 1999). It is therefore likely that once signal transduction pathways for nutrients are elucidated they will be found to interact and intersect with hormonal response pathways. As we have seen (above and Fig. 2), evidence for this already exists in the case of NO_3^- stimulation of lateral root growth in *Arabidopsis*, where the *AXR4* gene product appears to be a component of signalling pathways for both NO_3^- and auxin (Zhang et al., 1999).

Conclusions

It is clear that nutrients have profound effects on many aspects of root development. Furthermore, many of these effects are specific to particular nutrients and are strongly dependent on the genotype of the plant. In most cases, the developmental responses are adaptive, that is they serve to increase the efficiency of nutrient capture under situations of nutrient limitation, while minimizing on the input costs in terms of biomass (see Robinson, this volume). In these ways, the nutritional responses discussed in this review are quite distinct from simple growth responses or from non-specific effects such as might be associated with severe nutrient stress.

In general, the developmental processes that are sensitive to the nutrient supply are quantitatively modulated by it rather than being absolutely dependent on a particular nutritional signal. In this respect, nutritional regulation of development differs for example from the photomorphogenetic switch that occurs when dark-grown etiolated seedlings are exposed to light. However, there is a clearer parallel with another aspect of photomorphogenesis, the shade avoidance response, where the development of the shoot is modulated in a variety of quantitative ways by the direction and quality (red:far-red ratio) of the light source, enabling the plant to place its resource acquiring structures (leaves) in a more favourable position (Ballare, 1999). The shade avoidance response depends on the perception of the photons of different wavelengths by means of a family of photoreceptors known as phytochromes which are the first components of a complex signal transduction pathway (Furuya and Kim, 2000).

In view of the parallels with photomorphogenesis, and the accumulating evidence reviewed here that analogous pathways of signal perception and transduction are involved, we propose the term 'trophomorphogenesis' to describe changes in plant morphology arising from variations in the availability or distribution of nutrients in the environment. As we have seen from the above examples, the trophomorphogenic responses may be direct (localized responses resulting from changes in external nutrient concentration), or indirect (systemic responses resulting from changes in the plant's internal nutrient status), or sometimes a combination of the two. Straightforward growth responses not involving changes in plant morphology, and differences in plant morphology that could be attributed simply to effects of the nutrient supply on ontogenetic drift (see above), would naturally be excluded from this definition.

Clearly the picture presented in this review differs markedly from the conventional and still widely held view that developmental responses to the nutrient supply can be explained simply in terms of source–sink relationships and the reallocation of carbohydrate within the plant. The models we put forward make predictions for the existence of specific sensors for internal and external nutrient pools, intracellular and inter-organ signalling pathways and master regulatory genes that help to integrate the plant's response to multiple environmental signals (Fig. 3). By analogy with the progress currently being made in identifying components of the phytochrome signalling pathway (Furuya and Kim, 2000), we expect that forward and reverse genetic approaches in *Arabidopsis* and other species will enable these models to be put to the test and will ultimately lead to the elucidation of the nutrient signalling pathways.

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