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Root physiology – from gene to function

Preface

Introduction

In the last decade, enormous progress has been made on the physiology of plant roots, including on a wide range of molecular aspects. Much of that progress has been captured in the following papers, which highlight that the classical boundaries between physiology, biochemistry and molecular biology have vanished. Breakthroughs have been made possible through integration of molecular and whole-plant aspects. There has been a strong focus on a limited number of model species, including *Arabidopsis thaliana*. That focus has allowed greater insight into the significance of specific genes for plant development and functioning. However, many species are very different from *A. thaliana*, in that they are mycorrhizal, develop a symbiosis with N_2-fixing microsymbionts, or have other specialised root structures. Also, some have a much greater capacity to resist extreme environments due to specific adaptations, for example aerenchyma in the case of soil flooding, or are capable of tolerating a wide range of soil chemical constraints, such as acidity, salinity or heavy metal toxicities. Research on species other than *A. thaliana* is therefore pivotal, to develop new knowledge in plant sciences in a comprehensive manner. This fundamental new knowledge can be the basis for important applications in, e.g., agriculture and plant conservation. Although significant progress has been made, much remains to be learnt, especially for many aspects of root physiology. It is envisaged, however, that discoveries made in the recent past will likely lead to major breakthroughs in the next decade.

Resource acquisition and carbon metabolism

The discovery of the role of aquaporins in water transport in both animals and plants has been a major breakthrough for understanding plant water relations, in particular water uptake (Vandeleur et al., 2005). Aquaporins are water-channel proteins (Johansson et al., 2000; Maurel, 1997). Their name is somewhat unfortunate, since the term ‘porin’ is commonly used for proteins that allow the transport of large molecules in a fairly unspecific manner, whereas we now know that aquaporins, which belong to a class of proteins termed MIPs (membrane-intrinsic proteins), are rather specific. However, some can also transport other small molecules, e.g., glycerol (Zeuthen and Klaerke, 1999) or CO_2 (Uehlein et al., 2003). Knowledge on the regulation of aquaporins contributes to understanding plant responses to some abiotic stresses and might help in the design of new irrigation techniques to improve use of scarce water resources. Aquaporins are involved in the adjustment of the hydraulic conductivity of roots, and therefore in adjustments of the roots’ physiology during both phases of wet/dry cycles in natural communities and in horticultural crops with irrigation management using partial root-zone drying (Vandeleur et al., 2005). Wider implications of the regulation of aquaporins for acclimation during abiotic stress include the recent finding that the well-known decrease in root hydraulic conductance during flooding involves gating of a root aquaporin, due to cytosolic acidosis (Tournaire-Roux et al., 2003). Moreover, it can be speculated that aquaporins are important in hydraulic redistribution of water in the root–soil system. Aquaporins would allow a plant control over the exit of water from its roots into a soil with a more negative water potential than that of the roots themselves. This phenomenon, which was first described by Caldwell and Richards (1989) and termed ‘hydraulic lift’, is quite common in desert species with access to deep water (Yoder and Novak, 1999) and re-hydrates the rhizosphere of surface roots during the night. In contrast to 'hydraulic lift', for trees growing in a soil with a low conductance between the top and deeper layers, water movement *down* the profile might rely on hydraulic redistribution via the taproot (Burgess et al., 1998). So far, there are no data to support any speculations on involvement of aquaporins in hydraulic re-distribution, but it is expected that such information will become available during the next decade.

Major progress has been made on the physiology of uptake and metabolism of nitrogen (Miller and Cramer, 2005) and phosphorus (Raghothama and Karthikeyan, 2005; Smith, 2003a). Genes involved in the transport of these nutrients have been identified, and we are beginning to learn when and where these are expressed. We have also gained a much better understanding of the functioning of specialised roots involved in nutrient acquisition, such as the "proteoid" or "cluster" roots of Proteaceae and *Lupinus albus* (Lambers et al., 2003; Shane and Lambers, 2005). These cluster roots produce and exude vast amounts of carboxylates. Carboxylate release is not restricted to species with cluster roots, but it is the combination of their capacity to release carboxylates in an exudative burst and their structure that allows build-up of high concentrations in the rhizosphere. This ability provides these species with an opportunity to substantially modify their rhizosphere and 'mine' the soil in their immediate vicinity; they are particularly effective in the acquisition of scarcely available phosphorus and micronutrients. Some species belonging to the Cyperaceae have 'dauciform' (=carrot-shaped) roots (Davies et al., 1973; Lamont, 1974; Shane et al., 2005). In many ways, these dauciform roots function in much the same way as cluster roots; their development is suppressed at a high phosphorus supply and when formed they release citrate in an exudative burst (Shane et al., 2005; M.W. Shane and H. Lambers, unpubl.). The combination of biochemical/physiological and anatomical/morphological traits, which allows the build-up of high concentrations of exudates in the rhizosphere might be further exploited considering that the world's phosphorus reserves are dwindling (Vance, 2001).

Major phosphorus reserves are stored in agricultural soils, due to the application of phosphorus fertilisers ('phosphorus bank'). Depending on soil type and agronomic practices in the past, over 80% of applied phosphorus in fertilisers can be sorbed to soil particles, and hence, largely unavailable for most crop plants. We will need crop species with the root traits of Proteaceae and Cyperaceae to access that phosphorus bank. So far, only a limited number of species with cluster roots have been used in agriculture and horticulture, including *Macadamia integrifolia* (to produce nuts) (Firth et al., 2003), *Lupinus albus* (as a source of protein) (Gardner et al., 1981) and *Aspalanthus linearis* (to produce rooibos tea) (Ratshitaka et al., 2001). Most *Lupinus* species do not make cluster roots of the type produced by *L. albus*, but they do make structures of a similar function (Hocking and Jeffery, 2004). Other *Lupinus* species that are used as crop species, e.g., *L. angustifolius* make sand-binding roots (pers. observation), which may well serve a similar purpose. We are not aware of any species with dauciform roots being intentionally used in managed systems, although, given the relatively wide occurrence of dauciform roots in Cyperaceae (Shane et al., 2005) species with this root type might have been planted in some constructed wetlands. Making greater use of species with cluster roots or similar traits will be of economic benefit, since these plants will be able to access sparingly available phosphorus. In addition, there may be ecological benefits, because an improved capacity for phosphorus acquisition will decrease the need for high rates of phosphorus application, and hence potentially reduce run-off of phosphorus into streams and estuaries, thus limiting eutrophication.

Plants often acquire limiting resources in symbiosis with micro-organisms (Vessey et al., 2005). Our understanding of the legume–rhizobium symbiosis has increased dramatically, not in the least because of the powerful molecular techniques of transcriptomics and metabolomics. These approaches have made it possible to obtain a much improved overview of the metabolic differentiation during nodule development in *Lotus japonicus* (Colebatch et al., 2004). Approximately 860 genes are more highly expressed in nodules than in roots, including one third involved in metabolism and transport. More than 100 of the highly expressed genes encode proteins likely involved in signalling, or regulation of gene expression at the transcriptional or post-transcriptional level. The analysis showed clear signs of hypoxia in root nodules, as expected; in addition, there were numerous indications that nodule cells also experience phosphorus limitation. Much less is known about other N_2-fixing symbiosis (Vessey et al., 2005).

Mycorrhizal associations can be found in most vascular plant species, and this field of research has developed enormously in the recent past (Graham and Miller, 2005). Molecular tools have revolutionised studies of mycorrhizal diversity and abundance, improving knowledge on host specificity of the symbionts (Graham and Miller, 2005) and highlighting relationships between mycorrhizal fungi diversity as influencing the structure of some communities of vascular plants (e.g., Reynolds et al., 2003). Like the recent discoveries of genes for transport of mineral nutrients in plants (Miller and Cramer, 2005), rapid advances to elucidate genes regulating exchanges of molecules between plant hosts and arbuscular mycorrhizal (AM) fungi are being made. Our views on 'mycorrhizal dependency' need to be revisited, with the discovery that the micro-symbionts can be responsible for most of the phosphorus uptake when there is no, or only a minor, growth response (Smith et al., 2003b).

Carnivory of small animals is a specialised strategy used by some plant species to acquire inorganic nutrients (Adlassnig et al., 2005). Carnivorous species inhabit a range of nutrient-impoverished environments, ranging from fire-prone sand plains to acid peat bogs and aquatic habitats, with, as one might expect, a wide range of root sizes and structures (Adlassnig et al., 2005). In contrast with information available on their traps formed by shoot organs (Juniper et al., 1989), comparatively little is known about the physiology of roots of carnivorous plants; several studies have demonstrated the importance of the roots in water and nutrient uptake for at least some carnivorous species, but not in several others.

Since two books (Day et al., 2004; Lambers and Ribas-Carbo, 2005) dealing with plant respiration have recently been published in Govindjee's series *Advances in Photosynthesis and Respiration*, no review dealing with this aspect of root physiology has been included. Over the last decade or so, we have gained a much better understanding of the respiratory costs of nutrient acquisition in fast- and slow-growing herbaceous species (Poorter et al., 1991; Scheurwater et al., 1998). When plants are grown at a high supply of nitrate, the costs associated with nitrate uptake are considerably greater for inherently slow-growing species, due to a major efflux component (Scheurwater et al., 1999). That passive efflux needs to be compensated by a greater active influx, and thus accounts for greater respiratory costs per unit N acquired. However, greater efflux is not the cause of slower growth; rather, slower growth leads to greater efflux (Ter Steege et al., 1999) and hence greater respiratory costs (Nagel and Lambers, 2002). Considerable information has also become available on the quantitative significance of cyanide-resistant root respiration (Millenaar et al., 2001). Major progress is to be expected on the physiological significance of the alternative path, which has puzzled plant scientists for quite some time. That progress can be expected, because a technique to assess the activity of this path in intact tissues has become more widely available (Ribas-Carbo et al., 2005).

Perception of the abiotic and biotic root environment

We have gained an appreciation of the fact that roots 'sense' their environment, and that the plant responds in a feed-forward and adaptive manner. The feed-forward response when roots sense adverse conditions in the soil allows acclimation before a major disturbance of the plant's metabolism (Davies et al., 1994). When roots perceive that the soil is flooded, they respond with an enhanced concentration of ethylene in both the roots and above-ground plant parts. Ethylene induces the formation of aerenchyma in roots (Visser and Voesenek, 2005), and also affects adaptive processes in above-ground organs (Voesenek and Blom, 1999). Similarly, roots can sense the availability of water (Davies et al., 1994) as well as nitrogen and phosphorus (De Groot et al., 2003), and signal this information to the shoot, which responds in a feed-forward manner. In the case of water stress, the signalling molecule is ABA (Davies et al., 1994; Schurr et al., 1992). Cytokinins are involved in signalling the plant's N and P status (De Groot et al., 2003; Kuiper et al., 1989; Lambers et a1., 1998). These are some of many examples showing 'signalling' between roots and shoots. More details about signals and signal-transduction pathways are included in the review by Dodd (2005), highlighting that the signals need not always be one of the classical phytohormones, but can, for example, be nitrate or sugars also. Internal signalling in plants, as dependent on plant development and environmental conditions is a rapidly developing field, where much progress can be expected. The challenge will be to integrate the new information into improved crop production systems.

Sensing does not only involve resources, but also other chemical factors in the environment. Aluminium-resistant genotypes must be able to sense the presence of aluminium to respond with the release of aluminium-complexing carboxylates (Kochian et al., 2005). When roots release either mainly citrate or mainly malate, depending on soil pH (Veneklaas et al., 2003), they must be sensing the soil pH or a factor closely associated with it. Sensing environmental conditions is obviously crucial to performance of plants, although we still lack a thorough understanding of the exact mechanisms involved.

Signalling in plants is not only important between different organs of a plant, but also between hosts and parasitic plants (Okubara and Paulitz, 2005). Holoparasitic species are entirely dependent on a host for the completion of their life cycle (Lambers et al., 1998). If their seeds were to germinate in the absence of a suitable host, that would be fatal, especially for those that have extremely small seeds. In fact, both germination (Siame et al., 1993) and the formation of haustoria (Estabrook and Yoder, 1998; Smith et al., 1990), which connect the parasite with its host, depend on chemical signalling between host and parasite. This is an exciting and rapidly developing field. Knowledge of these interactions may appear esoteric, but major applications can be expected, because some parasitic species (e.g., *Striga* and *Orobanche* species) belong to the world's worst weeds (Emechebe et al., 2004; Marley et al., 2004; Rodriguez-Conde et al., 2004). Others (*Cistanche* species) are grown to produce medicine in north-eastern China (Geng et al., 2004). Low-cost and safe signalling molecules that trigger the germination of the seeds of parasitic pest species before crops are sown might be of enormous benefit, especially to farmers in developing countries.

Signalling is also important between hosts and their symbiotic micro-organisms, e.g., rhizobia (Vessey et al., 2005) and mycorrhizal fungi (Graham and Miller, 2005). The intricate interactions that precede the establishment of a functional symbiosis are best understood for the rhizobium–legume symbiosis (Esseling and Emons, 2004). They must also play a role in other symbiotic systems that fix dinitrogen, but the progress in that area has been much slower (Rai et al., 2000; Vessey et al., 2005). Somewhat more is known on signalling between hosts and some mycorrhizal fungi (Graham and Miller, 2005), but much remains to be discovered.

Plants growing in soil with adverse abiotic or biotic conditions

Some species or ecotypes are capable of growing in soils that are naturally enriched with heavy metals, e.g., serpentine or ultramafic soils. The metals may be 'excluded' or absorbed, and stored in compartments where they do not harm the plant's metabolism (Meharg, 2005). Recently, progress has been made on the mechanisms accounting for internal transport and storage of heavy metals as well as metal 'exclusion' (Meharg, 2005). Species or ecotypes that accumulate heavy metals to very high levels are called metallophytes. These are not restricted to soils naturally enriched with heavy metals, but are also found on sites contaminated by heavy metals, e.g., due to mining. Such metallophytes are very important to stabilise contaminated soil, and stop it from spreading over a larger area. Metallophytes have been proposed as a method to clean contaminated soil (phytoremediation) (Meharg, 2005) or extract metals from soil with the intention to mine the metals (phytomining) (Li et al., 2003). To be economically viable options, the metallophytes have to accumulate metals to very high concentrations and produce a lot of biomass in a relatively short time. However, most metallophytes are inherently slow-growing, most likely because they were selected in low-nutrient environments, which are typically inhabited by slow-growing species (Lambers and Poorter, 1992). Genotypes that are both metal resistant and productive need to be selected. Major new discoveries are to be expected in the next decade, but applications in the context of phytoremediation and phytomining would appear to be less promising than claimed when first proposed, unless combined with other profit-making operations, e.g., forestry (Robinson et al., 2003).

Mycorrhizas have been claimed to 'protect' higher plants from negative effects of heavy metals in soil (Leyval et al., 1997). It has also been shown that species that belong to a typically non-mycorrhizal family can be mycorrhizal if they are associated with soils with high levels of heavy metals. One example is for California serpentine grassland communities, where *Arenaria douglasii* (Caryophyllaceae) and *Streptanthus glandulosus* (Brassicaceae) were found to be mycorrhizal (Hopkins, 1987). Another example is for *Hakea verrucosa* (Proteaceae), occurring on nickel-containing ultramafic soils in Western Australia (Boulet and Lambers, 2005). These are exciting observations, from an evolutionary perspective as well as because of the possible implications for the rehabilitation of contaminated sites after mining.

Acid soils represent another stress to plant roots. It is not so much the low pH itself that causes the problems, but the fact that the solubility of specific metals strongly depends on pH (Kochian et al., 2005). In particular aluminium is considerably more soluble at low pH. Acid-resistant species typically are aluminium resistant. Resistance is at least partially based on 'exclusion', due to precipitation with citrate, malate or oxalate released from roots, depending on the species (Delhaize et al., 1993; Zheng et al., 1998). Some aluminium-resistant species also accumulate aluminium, and detoxify it internally as aluminium-carboxylate precipitates (Ma et al., 1997; Zheng et al., 1998). As for heavy metal resistance (Meharg, 2005), there is considerable genetic variation for aluminium exclusion (Delhaize et al., 1993; Kochian et al., 2005). This allows important application in agriculture, but care also has to be taken to minimise further soil acidification, which is a common trend in cropping systems (Lambers et al., 1998). Soil amelioration, e.g., using lime, remains important, but does not invariably address sub-soil acidity; therefore, aluminium-resistant genotypes would be important to develop.

Drought, salinity and flooding are abiotic stresses each of which influence plant species composition and productivity in natural and managed systems. Improved knowledge on physiological responses of roots to water stress, including root-to-shoot signalling (Dodd, 2005) should aid design of new irrigation techniques to improve use of scarce water resources (Vandeleur et al., 2005). Since various aspects of resistance to salinity have been reviewed recently (e.g., Munns, 2002; Tester and Davenport, 2003), and in a special issue dealing with dryland salinity in Australia (Lambers, 2003), salinity is not covered in this volume. Flooding regimes shape the composition of natural communities in some areas (Voesenek et al., 2004) and underpin rice production systems; soil waterlogging is also a problem in vast areas of irrigated and rainfed agriculture. Visser and Voesenek (2005) provide a comprehensive review on signals, and signal-transduction pathways, crucial to the perception and acclimation by plant roots to soil flooding. Hormones and signalling pathways that regulate traits for flooding resistance, such as adventitious rooting, aerenchyma formation for gas transport (Colmer and Greenway, 2005; Jackson and Armstrong, 1999) and root metabolism during O_2 deficiency (Gibbs and Greenway, 2003; Jackson and Ricard, 2003) are reviewed by Visser and Voesenek (2005). Substantial gains in knowledge in some areas are highlighted, as are emerging topics that are still poorly understood and will be priority areas for future research.

Roots frequently encounter adverse biotic conditions, due to the presence of microbial pathogens, nematodes, viruses and plant parasites (Okubara and Paulitz, 2005). Our understanding of these interactions has increased enormously, again, in part due to the development of new molecular tools. Developing resistance to root pests and diseases will continue to be important, as chemical protection is not always a desirable option.

Using new genotypes and combinations of crop species based on new ecophysiological information

Allelopathic interactions are very hard to demonstrate in nature, but they are very likely to occur, also in managed ecosystems (Lambers et al., 1998). The interactions may involve micro-organisms (Inderjit, 2005). Allelopathic interactions may account for the invasive nature of some weeds (Ridenour and Callaway, 2001). There are major possibilities for applications in agriculture. Accessions of wheat (*Triticum aestivun*) differ widely in their potential to inhibit seed germination of ryegrass (*Lolium rigidumi*) (Wu et al., 2000a), a major weed in Australia (Powles and Shaner, 2001). That variation appears to be associated with the release of allelochemicals of a phenolic nature (Wu et al., 2000b), although so far the phenolics have only been assessed in root tissue, not in exudates. Making a crop more competitive, by enhancing its capacity for interference competition, would reduce the need for herbicides.

Facilitation refers to positive effects of one plant on another (Callaway, 1995). It is equally difficult to demonstrate in natural systems as allelopathic interactions are (Hauggaard-Nielsen and Jensen, 2005), but there are numerous examples of increased yields when combinations of crop species are used (Karpenstein-Machan and Stuelpnagel, 2000; Zuo et al., 2000). Such agronomic practices, usually called intercropping, are used in the low-input systems of the tropics, where crops are harvested manually (Willey, 1979), and are also common in China (Zhang et al., 2004) where new intercropping systems continue to be developed (Guixin et al., 2004). If reliable systems can be developed to mechanically harvest intercropped species at the same time, then this would stimulate the development of the practice for broad-area agriculture in other countries.

Pasture agronomy already uses combinations of species in broad-area agriculture, but further research might enhance productivity of pasture systems if the best combinations of species, and perhaps genotypes within species, can be further refined. For example, when seedlings of mycorrhizal and non-mycorrhizal species are grown together, they tend to have negative effects on each other which are not seen when either seedlings of mycorrhizal species or ones of non-mycorrhizal species grow together (Francis and Read, 1994). The chemical basis of this interference is not known, but the observation may have major implications for plant functioning in natural or managed systems. It may mean that combinations of mycorrhizal and non-mycorrhizal species are less desirable for intercropping, and this will need to be addressed to enhance productivity of intercropping and pasture systems.

Perspectives

Many new discoveries are to be expected in the ecophysiology of roots of native and crop species. One can envisage many applications of the new fundamental knowledge. One area that has not been reviewed in this volume, because it is too new to have generated many publications, is that of signalling in tritrophic below-ground interactions. Similar above-ground interactions are well documented for interactions between plants, their herbivores and 'bodyguards' (Alborn et al., 1997; Kessler and Baldwin, 2001; Sabelis et al., 2001). The first exciting information is now becoming available on interactions between roots of *Thuja occidentalis*, which release chemicals upon attack by weevil larvae (*Otiorhynchus sulcatus*), to attract parasitic nematodes (*Heterorhabditis megidis*), which then prey on the weevil larvae (Van Tol et al., 2001). Similar tritrophic interactions appear to occur in *Zea mays* (T.C.J. Turlings, pers. comm.). It is to be expected that improved knowledge in this area should provide opportunities for applications in plant management systems, similar to those existing for above-ground tritrophic interactions (Turlings and Wäckers, 2004).

Major progress on understanding numerous aspects of root physiology, and under several important environmental constraints, has been made possible by close interactions between ecophysiologists, biochemists and molecular geneticists. These close interactions will be important to achieve new breakthroughs in yield improvement. Such breakthroughs are vitally important, if we are to produce enough food and fibre for the worlds growing population in a sustainable manner.

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