Root Exudation and Rhizosphere Biology[1]

Travis S. Walker, Harsh Pal Bais, Erich Grotewold, and Jorge M. Vivanco*

Department of Horticulture and Landscape Architecture (T.S.W., H.P.B., J.M.V.), Cellular and Molecular Biology Graduate Program (J.M.V.), and Graduate Degree Program in Ecology (J.M.V.), Colorado State University, Fort Collins, Colorado 80523; and Department of Plant Biology and Plant Biotechnology Center, The Ohio State University, Columbus, Ohio 43210 (E.G.)

Our understanding of the biology, biochemistry, and genetic development of roots has considerably improved during the last decade (Smith and Fedoroff, 1995; Flores et al., 1999; Benfey and Scheres, 2000). In contrast, the processes mediated by roots in the rhizosphere such as the secretion of root border cells and root exudates are not yet well understood (Hawes et al., 2000). In addition to the classical roles of providing mechanical support and allowing water/nutrient uptake, roots also perform certain specialized roles, including the ability to synthesize, accumulate, and secrete a diverse array of compounds (Flores et al., 1999). Given the complexity and biodiversity of the underground world, roots are clearly not passive targets for soil organisms. Rather, the compounds secreted by plant roots serve important roles as chemical attractants and repellants in the rhizosphere, the narrow zone of soil immediately surrounding the root system (Estabrook and Yoder, 1998; Bais et al., 2001). The chemicals secreted into the soil by roots are broadly referred to as root exudates. Through the exudation of a wide variety of compounds, roots may regulate the soil microbial community in their immediate vicinity, cope with herbivores, encourage beneficial symbioses, change the chemical and physical properties of the soil, and inhibit the growth of competing plant species (Nardi et al., 2000; Fig. 1A). The ability to secrete a vast array of compounds into the rhizosphere is one of the most remarkable metabolic features of plant roots, with nearly 5% to 21% of all photosynthetically fixed carbon being transferred to the rhizosphere through root exudates (Marschner, 1995).

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* Corresponding author; email jvivanco@lamar.colostate.edu; fax 970–491–7745.

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Although root exudation clearly represents a significant carbon cost to the plant, the mechanisms and regulatory processes controlling root secretion are just now beginning to be examined. Root exudates have traditionally been grouped into low- and high-M_r compounds. However, a systematic study to determine the complexity and chemical composition of root exudates from diverse plant species has not been undertaken. Low-M_r compounds such as amino acids, organic acids, sugars, phenolics, and various other secondary metabolites are believed to comprise the majority of root exudates, whereas high-M_r exudates primarily include mucilage (high-M_r polysaccharides) and proteins.

The rhizosphere is a densely populated area in which the roots must compete with the invading root systems of neighboring plant species for space, water, and mineral nutrients, and with soil-borne microorganisms, including bacteria, fungi, and insects feeding on an abundant source of organic material (Ryan and Delhaize, 2001). Thus, root-root, root-microbe, and root-insect communications are likely continuous occurrences in this biologically active soil zone, but due to the underground nature of roots, these intriguing interactions have largely been overlooked. Root-root and root-microbe communication can either be positive (symbiotic) to the plant, such as the association of epiphytes, mycorrhizal fungi, and nitrogen-fixing bacteria with roots; or negative to the plant, including interactions with parasitic plants, pathogenic bacteria, fungi, and insects. Thus, if plant roots are in constant communication with symbiotic and pathogenic organisms, how do roots effectively carry out this communication process within the rhizosphere?

A large body of knowledge suggests that root exudates may act as messengers that communicate and initiate biological and physical interactions between roots and soil organisms. This update will focus on recent advancements in root exudation and rhizosphere biology.

ROOT-RHIZOSPHERE COMMUNICATION

Survival of any plant species in a particular rhizosphere environment depends primarily on the ability of the plant to perceive changes in the local environment that require an adaptive response. Local

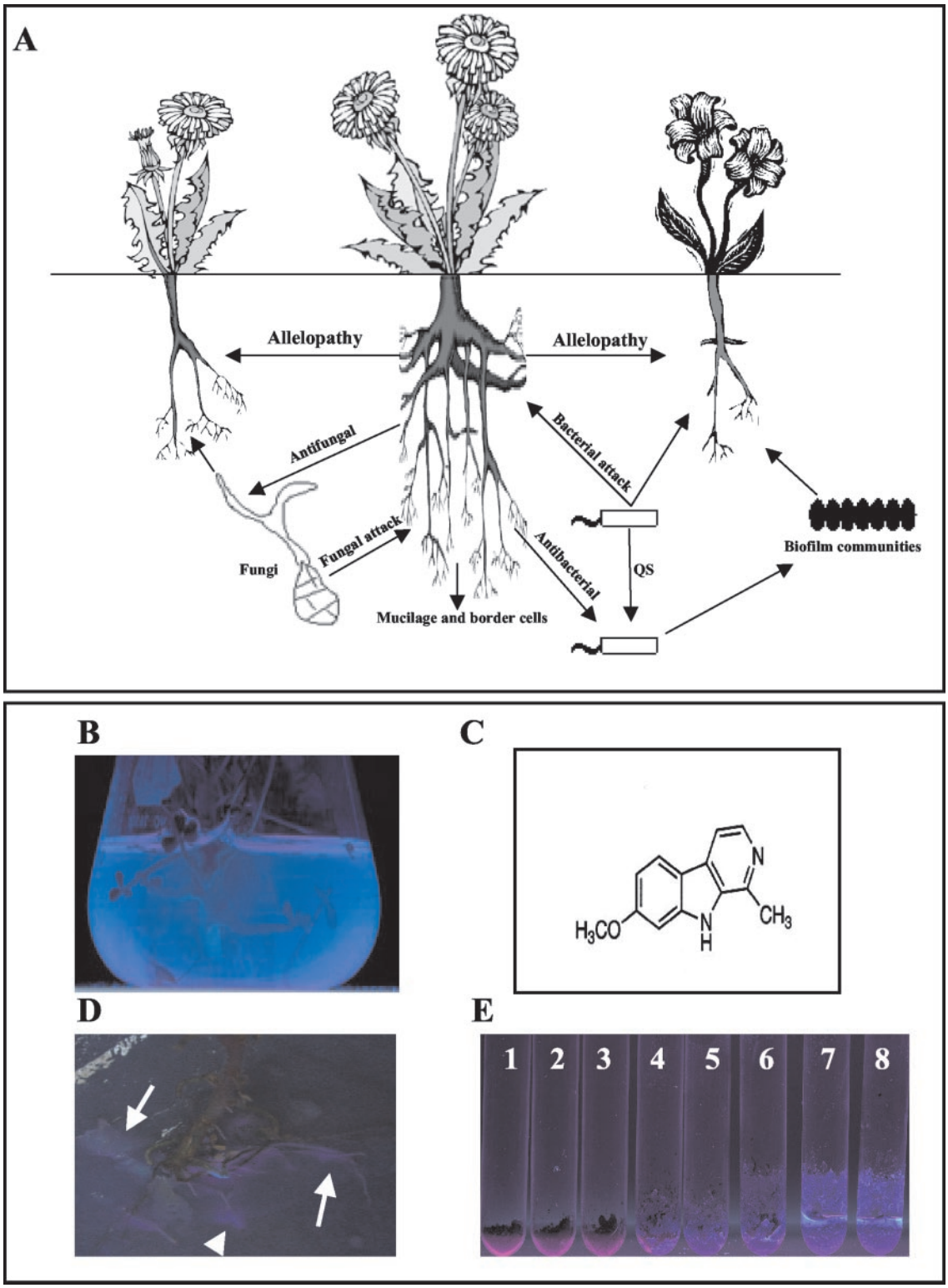

Figure 1. A, Representation of the complex interactions mediated by root exudates that take place in the rhizosphere between plant roots and other organisms. Organisms are not drawn to scale. QS, quorum sensing. B, In vitro culture of oca (*Oxalis tuberosa*) grown in sterile liquid medium under UV light exposure. C, Chemical structure of harmine as determined by ^{1}H and C^{13} NMR analysis. D, Fluorescent root exudates from *O. tuberosa* were observed bound to the blue germination paper under UV light exposure. E, Soil samples showing fluorescence obtained from greenhouse-grown oca plants. Samples were taken 5 cm from the stem girth of the plant, and the numbers (1–8) denote the depth by every 1 cm toward the top-layer soil. In vitro-grown oca plants and soil samples collected from oca's rhizosphere were visualized for blue-purplish fluorescence under UV light exposure with a short wave of UV approximately 254 nm.

changes within the rhizosphere can include the growth and development of neighboring plant species and microorganisms. Upon encountering a challenge, roots typically respond by secreting certain small molecules and proteins (Stintzi and Browse, 2000; Stotz et al., 2000). Root secretions may play symbiotic or defensive roles as a plant ultimately engages in positive or negative communication, depending on the other elements of its rhizosphere. In contrast to the extensive progress in studying plant-plant, plant-microbe, and plant-insect interactions that occur in aboveground plant organs such as leaves and stems, very little research has focused on root-root, root-microbe, and root-insect interactions in the rhizosphere. The following sections will examine the communication process between plant roots and other organisms in the rhizosphere.

Root-Root Communication

In natural settings, roots are in continual communication with surrounding root systems of neighboring plant species and quickly recognize and prevent the presence of invading roots through chemical messengers. Allelopathy is mediated by the release of certain secondary metabolites by plant roots and plays an important role in the establishment and maintenance of terrestrial plant communities. It also has important implications for agriculture; the effects may be beneficial, as in the case of natural weed control, or detrimental, when allelochemicals produced by weeds affect the growth of crop plants (Callaway and Aschehoug, 2000). A secondary metabolite secreted by the roots of knapweed (*Centaurea maculosa*) provides a classic example of root exudates exhibiting negative root-root communication in the rhizosphere. Recently, Bais et al. (2002c) identified (±)-catechin as the root-secreted phytotoxin responsible for the invasive behavior of knapweed in the rhizosphere. Interestingly, (−)-catechin was shown to account for the allelochemical activity, whereas (+)-catechin was inhibitory to soil-borne bacteria (Bais et al., 2002c). In addition to racemic catechin being detected in the exudates of in vitro-grown plants, the compound was also detected in soil extracts from knapweed-invaded fields, which strongly supported the idea that knapweed's invasive behavior is due to the exudation of (−)-catechin. Moreover, this study established the biological significance of the exudation of a racemic compound such as catechin, demonstrating that one enantiomer can be responsible for the invasive nature of the plant, whereas the other enantiomer can contribute to plant defense.

Although studies have reported the biosynthesis of the common enantiomer (+)-catechin, little is known regarding the synthesis of (−)-catechin or (±)-catechin as natural products. One possibility is that (+)-catechin production is followed by racemization in the root or during the exudation process. Alternatively, there could be a deviation from the normally observed stereo- and enantiospecific biosynthesis steps. The flavonols kaempferol and quercetin are generally perceived as final products, rather than intermediates, in the pathway (Winkel-Shirley, 2001). The correlation of these experiments to the root exudation process has yet to be determined, but the data should provide a starting point for further studies on the characterization of specific committed steps in the synthesis of racemic catechin in knapweed roots.

The above example demonstrates how plants use root-secreted secondary metabolites to regulate the rhizosphere to the detriment of neighboring plants. However, parasitic plants often use secondary metabolites secreted from roots as chemical messengers to initiate the development of invasive organs (haustoria) required for heterotrophic growth (Keyes et al., 2000). Some of the most devastating parasitic plants of important food crops such as maize (*Zea mays*), sorghum (*Sorghum bicolor*), millet (*Panicum milaceum*), rice (*Oryza sativa*), and legumes belong to the Scrophulariaceae, which typically invade the roots of surrounding plants to deprive them of water, minerals, and essential nutrients (Yoder, 2001). It has been reported that certain allelochemicals such as flavonoids, *p*-hydroxy acids, quinones, and cytokinins secreted by host roots induce haustorium formation (Estabrook and Yoder, 1998; Yoder, 2001), but the exact structural requirements of the secreted compounds for haustorium induction is not fully understood.

Root-Microbe Communication

Root-microbe communication is another important process that characterizes the underground zone. Some compounds identified in root exudates that have been shown to play an important role in root-microbe interactions include flavonoids present in the root exudates of legumes that activate *Rhizobium meliloti* genes responsible for the nodulation process (Peters et al., 1986). Although the studies are not yet conclusive, these compounds may also be responsible for vesicular-arbuscular mycorrhiza colonization (Becard et al., 1992, 1995; Trieu et al., 1997). In contrast, survival of the delicate and physically unprotected root cells under continual attack by pathogenic microorganisms depends on a continuous "underground chemical warfare" mediated by secretion of phytoalexins, defense proteins, and other as yet unknown chemicals (Flores et al., 1999).

The unexplored chemodiversity of root exudates is an obvious place to search for novel biologically active compounds, including antimicrobials. For instance, Bais et al. (2002b) recently identified rosmarinic acid (RA) in the root exudates of hairy root cultures of sweet basil (*Ocimum basilicum*) elicited by fungal cell wall extracts from *Phytophthora cinnamoni*. Basil roots were also induced to exude RA by fungal

in situ challenge with *Pythium ultimum*, and RA demonstrated potent antimicrobial activity against an array of soil-borne microorganisms including *Pseudomonas aeruginosa* (Bais et al., 2002b). Similar studies by Brigham et al. (1999) with *Lithospermum erythrorhizon* hairy roots reported cell-specific production of pigmented naphthoquinones upon elicitation, and other biological activity against soil-borne bacteria and fungi. Given the observed antimicrobial activity of RA and naphthoquinones, these findings strongly suggest the importance of root exudates in defending the rhizosphere against pathogenic microorganisms. Moreover, the aforementioned studies complement earlier research that mainly focused on the regulation and production of these compounds by providing valuable insights into the biological importance of RA and shikonin.

Both Gram-negative and -positive bacteria, including important plant pathogenic bacteria such as *Erwinia* spp., *Pseudomonas* spp., and *Agrobacterium* spp., possess quorum-sensing systems that control the expression of several genes required for pathogenicity (for review, see Fray, 2002). Quorum sensing is a form of cell-cell communication between bacteria mediated by small diffusible signaling molecules (autoinducers); these are generally acylated homo-Ser lactones (AHLs) for Gram-negative bacteria and peptide-signaling molecules for Gram-positive bacteria. Upon reaching a threshold concentration at high-population densities, an auto-inducer then activates transcriptional activator proteins that induce specific genes. Thus, intercellular signals enable a bacterial population to control the expression of genes in response to cell density. A recent review by Fray (2002) reported that AHL-producing transgenic tobacco plants restored pathogenicity to an avirulent AHL-deficient *Erwinia carotovora* mutant. Root exudates from pea (*Pisum sativum*) seedlings were found to contain several bioactive components that mimicked AHL signals in well-characterized bacterial reporter strains, stimulating AHL-regulated behaviors in some strains while inhibiting such behaviors in others. The chemical nature of such active mimic secondary metabolites is currently unknown (Teplitski et al., 2000; Knee et al., 2001). However, it was also reported that crude aqueous extracts from several plant species exhibited AHL inhibitory activity. Thus, it is possible that roots may have developed defense strategies by secreting compounds into the rhizosphere that interfere with bacterial quorum-sensing responses such as signal mimics, signal blockers, and/or signal-degrading enzymes, but future studies are required to isolate and characterize these compounds.

Root-Insect Communication

The study of plant-insect interactions mediated by chemical signals has largely been confined to leaves and stems, whereas the study of root-insect communication has remained largely unexplored due to the complexity of the rhizosphere and a lack of suitable experimental systems. However, root herbivory by pests such as aphids can cause significant decreases in yield and quality of important crops including sugar beet (*Beta vulgaris*), potato (*Solanum tuberosum*), and legumes (Hutchison and Campbell, 1994). One attempt to study root-insect communication was developed by Wu et al. (1999) using an in vitro coculture system with hairy roots and aphids. In this study, it was observed that aphid herbivory reduced vegetative growth and increased the production of polyacetylenes, which have been reported to be part of the phytoalexin response (Flores et al., 1988). In a more recent study, Bais et al. (2002a) reported the characterization of fluorescent β-carboline alkaloids from the root exudates of *O. tuberosa* (oca). The main fluorescent compounds were identified as harmine (7-methoxy-1-methyl-β-carboline) and harmaline (3, 4-dihydroharmine; Bais et al., 2002a; Fig. 1, B–E). In addition to their fluorescent nature, these alkaloids exhibit strong phototoxicity against a polyphagous feeder, *Trichoplusia ni*, suggesting their insecticidal activity may be linked to photoactivation (Larson et al., 1988). The Andean highlands, where *O. tuberosa* is primarily cultivated, are subjected to a high incidence of UV radiation, and it was observed that the strongest fluorescence intensity occurred with oca varieties that showed resistance to the larvae of *Mycrotrypes* spp., the Andean tuber weevil (Flores et al., 1999). These data suggest that UV light penetrating soil layers could photoactivate fluorescent β-carboline alkaloids secreted by oca roots to create an insecticidal defense response.

ALTERATION OF SOIL CHARACTERISTICS THROUGH EXUDATION

As a consequence of normal growth and development, a large range of organic and inorganic substances are secreted by roots into the soil, which inevitably leads to changes in its biochemical and physical properties (Rougier, 1981). Various functions have been attributed to root cap exudation including the maintenance of root-soil contact, lubrication of the root tip, protection of roots from desiccation, stabilization of soil micro-aggregates, and selective adsorption and storage of ions (Griffin et al., 1976; Rougier, 1981; Bengough and McKenzie, 1997; Hawes et al., 2000). Root mucilage is a reasonably studied root exudate that is believed to alter the surrounding soil as it is secreted from continuously growing root cap cells (Vermeer and McCully, 1982; Ray et al., 1988; McCully, 1995; Sims et al., 2000). Soil at field capacity typically possesses a matric potential of −5 to −10 kPa (Chaboud and Rougier, 1984). It has been speculated that as the soil dries and its hydraulic potential decreases, exudates will subsequently

begin to lose water to soil. When this occurs, the surface tension of the exudates decreases and its viscosity increases. As the surface tension decreases, the ability of the exudates to wet the surrounding soil particles will become greater. In addition, as viscosity increases, the resistance to movement of soil particles in contact with exudates will increase, and a degree of stabilization within the rhizosphere will be achieved. For instance, McCully and Boyer (1997) reported that mucilage from the aerial nodal roots of maize has a water potential of −11 Mpa, indicating a large capacity for water storage when fully hydrated, whereas the mucilage loses water to the soil as it begins to dry.

This speculation supports the idea that root exudates could play a major role in the maintenance of root-soil contact, which is especially important to the plant under drought and drying conditions, when hydraulic continuity will be lost. The largest, most coherent soil rhizosheaths are formed on the roots of grasses in dry soil (Watt et al., 1994). However, sheath formation requires fully hydrated exudates to permeate the surrounding soil particles that are then bonded to the root and each other as the mucilage dries. Young (1995) found that rhizosheath soil was significantly wetter than bulk soil and suggested that exudates within the rhizosheath increase the water-holding capacity of the soil. Furthermore, it has recently been proposed that in dry soil, the source of water to hydrate and expand exudates is the root itself. Modern cryo-scanning microscopy has helped researchers determine that the rhizosheath of a plant is more hydrated in the early morning hours compared with the midday samplings (McCully and Boyer, 1997). This implies that the exudates released from the roots at night allow the expansion of the roots into the surrounding soil. When transpiration resumes, the exudates begin to dry and adhere to the adjacent soil particles. Thus, the rhizosheath is a dynamic region, with cyclic fluctuations in hydration content controlled to some extent by roots.

Taken together, these studies indicate that root exudation plays a major role in maintaining root-soil contact in the rhizosphere by modifying the biochemical and physical properties of the rhizosphere and contributing to root growth and plant survival. However, the exact fate of exuded compounds in the rhizosphere, and the nature of their reactions in the soil, remains poorly understood.

CELLULAR MECHANISMS OF ROOT EXUDATION

Subcellular Trafficking of Exuded Metabolites

Despite the ecophysiological significance of plant-secreted compounds and the large number of compounds that plant cells produce, very little is currently known about the molecular mechanisms for the trafficking of phytochemicals. In at least some plants, channels are likely to be involved in the secretion of organic acids normally present at high levels in the cytoplasm. A good example is provided by the exudation of citrate, malate, and related organic acids by maize and wheat (*Triticum aestivum*) in response to high Al^{3+} concentrations (Ma et al., 2001). However, plants have the potential to express 100,000 compounds, primarily derived from secondary metabolism (Verpoorte, 2000), many of them with cytotoxic activities that would prevent their accumulation in the cytoplasm. The speculation that phytochemicals are transported from the site of synthesis to the site of storage by vesicles or specialized organelles is gaining momentum as evidence accumulates regarding the presence of intracellular bodies in plant cells induced to accumulate large quantities of secondary metabolites (Grotewold, 2001). For example, it has long been known that specific steps of the isoquinoline alkaloid biosynthetic pathway are sequestered in alkaloid vesicles and that pathway intermediates must traffic from one subcellular compartment to another by mechanisms that prevent their free diffusion in the cytosol (Facchini, 2001). Subcellular inclusions that accumulate 3-deoxy anthocyanidin flavonoid phytoalexins are observed in sorghum leaves infected by the fungus *Colletotrichum graminicola* (Snyder and Nicholson, 1990). These inclusions are similar to the anthocyanoplasts observed in maize cells expressing the C1 and R regulators of anthocyanin accumulation (Grotewold et al., 1998).

Root exudates often include phenylpropanoids and flavonoids, presumably synthesized on the cytoplasmic surface of the endoplasmic reticulum (ER; Winkel-Shirley, 2001). For example, the flavone luteolin, secreted by alfalfa (*Medicago sativa*) seedlings and seed coats, provides one of the signals that induces the nodulation genes in *R. meliloti* (Peters et al., 1986). Cytotoxic and antimicrobial catechin flavonoids are secreted by the roots of knapweed plants (Bais et al., 2002c). Although the mechanisms by which these compounds are transported from the ER to the plasma membrane are not known, it is possible that they are transported by ER-originating vesicles that fuse to the cell membrane and release their contents.

Vesicles with the above-described properties and containing green autofluorescent compounds have been identified in maize cells ectopically expressing the P regulator of 3-deoxy flavonoid biosynthesis (Grotewold et al., 1998). These vesicles are likely to originate from the ER, as suggested by the presence of green fluorescence inside specific regions of the ER after treatment with brefeldin A. The vesicles fuse and form large green fluorescent bodies that migrate to the surface of the cell and fuse to the cell membrane and release the green fluorescent compound to the cell wall (Grotewold et al., 1998). Interestingly, the accumulation of the green fluorescence in the cell wall is increased by treatment with Golgi-disrupting agents, such as brefeldin A or monensin, suggesting

a trans-Golgi network-independent pathway for the secretion of these compounds. Cultured cells of maize ectopically expressing P also accumulate increased quantities of yellow autofluorescent compounds that are targeted to the central vacuole by subcellular structures that resemble anthocyanoplasts (Grotewold et al., 1998). The use of these autofluorescent compounds, or the fluorescent β-carbolines present in exudates of *O. tuberosa* roots (Bais et al., 2002a), should greatly increase the opportunities available to study the molecular mechanisms underlying the secretion of phytochemicals.

ATP-Binding Cassette (ABC) Transporter as an Alternative to Vesicular Trafficking

The previous section highlighted the possibility of vesicular trafficking and fusion as a cellular mechanism responsible for root exudation, but could other mechanisms also be responsible once the compounds reach the membrane? For example, the involvement of membrane transporters such as the ABC transporters might be responsible for the secretion of root-secreted compounds. The ABC superfamily of membrane transporters is one of the largest protein families, and its members can be found in animals, bacteria, fungi, and plants. ABC transporters use ATP hydrolysis to actively transport chemically and structurally unrelated compounds from cells (Martinoia et al., 2002). The recent completion of the Arabidopsis genome research project (Arabidopsis Genome Initiative, 2000) revealed that Arabidopsis contains 53 putative ABC transporter genes. However, the protein localization and function of most of these genes are largely unknown (Martinoia et al., 2002). Most of the plant ABC transporters characterized to date have been localized in the vacuolar membrane and are believed to be responsible for the intracellular sequestration of cytotoxins (Theodoulou, 2000).

Currently, very little is known about plant plasma membrane ABC transporters, but the Arabidopsis AtPGP1, localized to the plasma membrane (Sidler et al., 1998), has been shown to be involved in cell elongation by actively pumping auxin from its site of synthesis in the cytoplasm to appropriate cells (Noh et al., 2001). Working on the assumption that plasma membrane ABC transporters might be involved in the secretion of defense metabolites, and their expression may be regulated by the concentration of these metabolites, Jasinski et al. (2002) identified a plasma membrane ABC transporter (NpABC1) from *Nicotiana plumbaginifolia* by treating cell cultures with various secondary metabolites. Interestingly, addition of sclareolide, an antifungal diterpene produced at the leaf surface of *Nicotiana* spp. (Baily et al., 1975), resulted in the expression of NpABC1 (Jasinski et al., 2002). These findings suggest that NpABC1 and likely other plasma membrane ABC transporters are involved in the secretion of secondary metabolites involved in plant defense, but further studies are required to positively identify plasma membrane ABC transporters involved in root exudation of specific compounds.

SPATIAL LOCALIZATION OF ROOT EXUDATES

Major differences in root architecture exist among plant species (Fitter, 1996), and because different root classes of the same plant exploit different portions of the soil and are subject to different external signals, it has been speculated that they may have different metabolic activity. In accordance, it has been observed that nutrient influx by plant roots is heterogeneous in time and space. In the common bean (*Phaseolus vulgaris*), the basal roots have a consistently higher influx rate of nutrients than the other root classes (i.e. adventitious, lateral, and tap; Liao et al., 2001; Rubio et al., 2001). This characteristic could be beneficial for the plant because basal roots generally explore the topsoil, where the majority of available nutrients are located (Lynch and Brown, 2001). Furthermore, Russell and Sanderson (1967) found a large variation in the phosphorus influx rate among seminal, nodal, and lateral roots of barley (*Hordeum vulgare*). Kuhllmann and Barraclough (1987) observed that the rates of nitrogen uptake by nodal roots of wheat were up to 6 times higher than those of seminal roots, but the uptake ratio of potassium differed to a much smaller extent among root classes. Despite this large body of evidence linking root architecture with root absorption of nutrients, the effect of root architecture on root exudation has been virtually unexplored.

Another long-standing question is related to the pattern of root exudation along the longitudinal root axis. From the base to the tip, most root classes can be clearly divided into different sections based on marked dissimilarities in their anatomical characteristics (Gilroy and Jones, 2000). These sections are typically the root tip, the elongation zone, the maturation zone, and the matured zone. The root tip includes two subsections: the root cap and the meristematic region. In the elongation zone, located right behind the root tip, no cell division occurs, but there is vigorous cell elongation activity. The next section is the maturation zone, where xylem vessels are completely differentiated. Here, some epidermal cells elongate perpendicularly toward the rhizosphere; these cells are known as the root hairs. After a short period of life, root hairs die and this region becomes the mature zone of the root. The degree of cell vacuolization increases from the root tip (where no cell vacuoles are present) to the base of the root. How this anatomical heterogeneity along the root axis relates to the metabolic activity of the roots has concerned researchers for decades (Prevot and Steward, 1936).

Although the stages of aging correlate well with the metabolic activity of the root, it is widely recog-

nized that the gradual maturation of root tissues along the root axis is not the only source of variation of metabolic activity (Eshel and Waisel, 1996). Although the large carbon demand in the apical zone has been traditionally attributed to high biosynthesis rates, it may also be due to an active root exudation process. In the case of the influx processes, the absorption of sulfur is highest in the elongation zone immediately behind the meristematic region (Holobrada, 1977) and that of iron at the apical zones of the roots. In the case of nitrogen or phosphorus, contrasting results have been found (Colmer and Bloom, 1998).

Much less attention has been focused on the spatial localization of the root exudation process. The scarce information available suggests that the pattern of exudation is not homogeneous along the root axis. Release of phytosiderophores in response to iron deficiencies appears to be concentrated in the apical zones of the root (Marschner et al., 1987). Release of organic anions would also follow a heterogeneous pattern along the root (Hoffland et al., 1989), which is consistent with the presence of a pH gradient from the tip to the base of the root (Fischer et al., 1989). On the other hand, based on the type of soil and its surface resistance, root tips may secrete a battery of compounds to soften the soil to facilitate root growth (Morel et al., 1991). Although such a mechanism has been hypothesized for decades, the chemicals involved in this phenomenon have yet to be identified. An understanding of the spatial and physical localization of the sites of exudation in the roots will facilitate the elucidation of plant-microbe and plant-plant interactions. For instance, external signals from pathogens and invasive plants may determine the zone of the root where the release of exudates takes place. If there is any relationship between the presence of pathogens and invasive plants with the localization of root exudation process, it is virtually unknown at the present time.

FINAL REMARKS

Due to significant advances in root biology and current National Science Foundation-funded projects on genomics of root-specific traits, roots are no longer considered an unexplored biological frontier. In contrast, knowledge of rhizospheric processes mediated by root exudates has not developed at the same pace. As highlighted in this update, several lines of evidence indicate that root exudates in their various forms may regulate plant and microbial communities in the rhizosphere. It is worth mentioning that most microbes live in the soil, but just a few of these organisms have developed compatible interactions with specific plants to become successful plant pathogens. Instead, the vast majority of microbes exhibit incompatible interactions with plants, which could be explained by the constant and diverse secretion of antimicrobial root exudates. The understanding of the biology of root exudation processes may contribute to devising novel strategies for improving plant fitness and the isolation of novel value-added compounds found in the root exudates.

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