Phytoremediation is the use of vegetation for in situ treatment of contaminated soils, sediments, and water. It is applicable at sites containing organic, nutrient, or metal pollutants that can be accessed by the roots of plants and sequestered, degraded, immobilized, or metabolized in place. In the last few years a greater understanding has been achieved regarding the uptake and metabolism of organic xenobiotic chemicals by plants, especially chlorinated solvents, some pesticides, and explosives compounds (1–8). These chemicals contaminate a large number of hazardous waste sites. In this review we focus on recent advances in the understanding of sorption, uptake, phytotransformation, and toxicity of such chemicals, especially chlorinated aliphatics.

Phytoremediation is popular because of its cost-effectiveness, aesthetic advantages, and long-term applicability (2). Applications include hazardous waste sites where other methods of treatment are too expensive or impractical, low-level contaminated sites where only “polishing treatment” is required over long periods of time, and sites where phytoremediation can be used in conjunction with other technologies as a final cap. Limitations of the technology include the potential for introducing the contaminant or its metabolites into the food chain, long cleanup times required to achieve regulatory action levels, and toxicity encountered in establishing and maintaining vegetation at waste sites.

Plants have shown the capacity to withstand relatively high concentrations of organic xenobiotic chemicals without toxic effects (5,9), and in some cases they can take up and convert chemicals quickly to less toxic metabolites (3,10–13). In addition, they stimulate the degradation of organic chemicals in the rhizosphere by the release of root exudates and enzymes and the resulting buildup of organic carbon in the soil (1,14,15). When toxicity is an issue, nutrients and soil amendments can be added to ameliorate toxicity and establish vegetation at waste sites. Once the plants are established and contaminant concentrations are somewhat diminished, vigorous growth and remediation can occur. For metal contaminants, plants show the potential for phytoextraction (uptake and recovery of metals into above-ground biomass), filtering metals from water onto root systems (16) or stabilizing wastes by hydraulic and erosional control at the site (phytostabilization) (16–18). Table 1 provides a summary of some phytoremediation applications and plants that have been used.

**Organic Chemicals and Sorption to Roots**

Organic chemicals may sorb to roots and be translocated, metabolized, or transpired (volatilized) by plants. The first step is sorption to roots. When chemical contaminants in soil water or groundwater come into contact with roots, they may sorb or bind to the root structure and cell walls. Hemicellulose in the cell wall and the lipid bilayer of plant membranes can bind hydrophobic organic chemicals effectively. Such sorption should be relatively reversible and can be measured using standard sorption isotherms. Figure 1 is an example of a sorption isotherm after 48 hr for 1,4-dichlorobenzene in a hydroponic solution with fresh hybrid poplar roots (Populus deltoides × nigra, DN-34) grown both in the laboratory and in the field at Amana, Iowa (19). The field roots contained higher lipid content and surface area, accounting for the enhanced partitioning with dichlorobenzene.

Briggs et al. (9) defined the root concentration factor (RCF) as the ratio of organic chemical sorbed on the root (milligrams per kilogram of fresh root tissue) to that in hydroponic solution (milligrams per liter). Thus, the slopes of the linear sorption isotherms in Figure 1 are measures of the RCF and have units of liters per kilogram. Briggs et al. measured the RCF of substituted phenyl areas on barley roots and determined that hydrophobic organic chemicals were the most strongly sorbed. Hydrophobicity was related to the octanol–water partition coefficient (log Kow) of the organics, and log RCF was correlated with log Kow via a least squares regression equation. The greater the hydrophobicity of the chemical (as measured by the Log Kow), the greater its tendency to partition out of the aqueous phase and onto roots. Burken and Schnoor (5) published a similar relationship for organic contaminants typically found at waste sites, using hybrid poplar roots grown hydroponically. Both relationships indicate that organic chemicals with log Kow > 3.0 are highly sorbed by roots.

Log (RCF – 3.0) = 0.65 log Kow – 1.57 (5)

Log (RCF – 0.82) = 0.77 log Kow – 1.52 (9)

These two equations are plotted in Figure 2, together with data from selected organic chemicals on poplar roots from Burken and Schnoor (5). Selected organic chemicals, their physicochemical properties, and measured RCF values on hybrid poplar roots...


**Uptake and Translocation**

Rooted vascular plants must take up water and nutrients for growth. Nutrients are transported into cells through channels in membranes or via membrane-bound proteins that bind the chemical and transport it into the cell (active transport). Base metal cations (Ca2+, Mg2+, K+, and Na+) are taken up by active transport mechanisms. Organic chemicals can be taken up by plants via diffusion (passive uptake) through cell walls and membranes. In this case there may exist an optimum hydrophobicity that allows the chemical to bind to the lipid bilayer of the membrane but not too strongly for transport to be facilitated.

Direct uptake of organic compounds by plants is a surprisingly efficient removal mechanism from shallow contaminated sites with moderately hydrophobic organic chemicals (log Kow = 1–3.5). These include most benzene, toluene, ethylbenzene, and xylene (BTEX) chemicals, chlorinated solvents, and short-chain aliphatic hydrocarbons. Hydrophobic chemicals (log Kow > 3.5) are bound so strongly to the surface of roots and soils that they cannot be translocated easily within the plant, and chemicals that are quite water soluble (log Kow < 1.0) are not sufficiently sorbed to roots nor actively transported through plant membranes (9). Hydrophobic chemicals (log Kow > 3.5) are candidates for phytostabilization and/or rhizosphere bioremediation by virtue of their long residence times in the root zone.

Uptake of chemicals into plants through roots depends on the plant’s uptake efficiency, the transpiration rate, and the concentration of chemical in soil water (20):

\[ U = (TSCF) (T) (C), \]

where \( U \) is the the rate of chemical uptake by plant in milligrams per day, TSCF is the efficiency of uptake (dimensionless), \( T \) is the transpiration rate in liters per day, and \( C \) is the soil water concentration of chemical in milligrams per liter.

Uptake efficiency for rooted vascular plants (with chemicals that are not transformed immediately) is defined as the transpiration fraction of the sorbed chemical.

**Figure 1.** Isotherm for the sorption of 1,4-dichlorobenzene on hybrid poplar roots (Populus deltoides x nigra, DN-34). Hydroponically grown roots and roots extracted from 5-year-old trees in the field (1.0 g of fresh roots in 10-ml scintillation vials) were exposed to 0.1–10 mg/L of cold chemical or 14C-radiolabeled chemical. Sorption was measured by difference in solution after equilibrium concentrations were achieved (usually 48 hr) and by radiochemical methods. The RCF is the slope of the line: 26.4 mL/g for field roots and 7.1 mL/g for hydroponic roots (10).

**Figure 2.** RCF as a function of the Log Kow for selected xenobiotic chemicals. The solid line is the best fit expression for the chemicals shown with hybrid poplar trees (9). The dotted line represents the results from Briggs et al. (9) for substituted phenylureas on barley for comparison purposes. Data modified from Briggs et al. (9) and Burken and Schnoor (9).

**Table 1.** Typical plants used in various phytoremediation applications.

| Application       | Media                                      | Contaminates                              | Typical plants                        |
|-------------------|--------------------------------------------|-------------------------------------------|---------------------------------------|
| **Phytotransformation** | Soil, groundwater, landfill leachate, land application of wastewater | Herbicides; chlorinated aliphatics (e.g., TCE), aromatics (e.g., BTEX), ammonia wastes (TNT, RDX, HMX, perchlorate); nutrients (nitrate, ammonium, phosphate) | Phreatophytic trees (Salix family, including poplar, willow, cottonwood); grasses (rye, fescue, Bermuda grass, sorghum, switchgrass, Reed canary grass); legumes (clover, alfalfa, cowpea) |
| **Rhizosphere bioremediation** | Soil, sediments, land application, confined disposal facilities | Biodegradable organics (BTEX, TPH, PAHs, PCBs, pesticides) | Grasses with fibrous roots (Bermuda, fescue, ryegrass); phenolics releasers (mulberry, apple, osage orange); phytotoxicity trees |
| **Phytostabilization** | Soils                                       | Metals (Pb, Cd, Zn, As, Cu, Cr, Se, U); hydrophobic organics that are not biodegradable | Phreatophytic trees for hydraulic control; grasses with fibrous roots for erosion control |
| **Phytoremediation** | Soil, sediments, brownfields               | Metals (Pb, Cd, Zn, Ni, Cu)               | Indian mustard (Brassica juncea); sunflowers (Helianthus spp.); Thlaspi canadensis |
| **Rhizofiltration** | Groundwater, wastewater through constructed wetlands | Metals (Pb, Cd, Cu, Ni, Zn); radionuclides, hydrophobic organics | Aquatic plants: emergents (bullrush, cattail, coontail, pond weed, arrowroot); submerged plants (algae, stonewort, parrot feather, Hydra spp.) |
| **Phytovolatilization** | Soils and sediments                         | Selenium, arsenic, mercury, volatile organic compounds (e.g., MTBE) | Brassica juncea; wetlands plants; phreatophytic trees for groundwater capture |

**Abbreviations:** BTEX, benzene, toluene, ethylbenzene, and total xylene. HMX, octahydro-1,3,5,7-tetracyclocyclohexadiene. PCBs, polychlorinated biphenyls. RDX, hexahydro-1,3,5-trinitro-1,3,5-triazine. TCE, trichloroethylene. TNT, 2,4,6-trinitrotoluene. TPH, total petroleum hydrocarbons.
stream concentration factor (TSCF). TSCF is the ratio of the concentration in the transpiration stream of the plant to the concentration in soil water, and TSCF depends on physicochemical properties, chemical speciation, and the plant itself. Some measured values appear in Table 2. TSCF can vary from zero (no uptake) to 1.0 (uptake at the same concentration as the soil water concentration). Chemicals that react biochemically at the root–water interface do not follow the above relationship because uptake is determined by site binding and biochemical reaction and not by the rate of passage through membranes into the transpiration stream. Transpiration rate is a key variable that determines the rate of chemical uptake for a given phytoremediation application and depends on the plant type, leaf area, nutrients, soil moisture, temperature, wind conditions, and relative humidity. High transpiration corresponds to rapid uptake, and this is why fast-growing phreatophytes (e.g., hybrid poplars and willows) are frequently employed in phytoremediation applications.

TSCFs have been measured for herbicide-related chemicals (substituted phenylureas and α-methylcarbamoyloximes) with crop species (barley) by Briggs and coworkers (5). Burken and Schnoor (5) measured a wide variety of chemicals found at hazardous waste sites with hybrid poplar trees. Both relationships predict a large uptake for chemicals in the moderately hydrophobic range (log $K_{ow} = 1.0$–3.5).

$$TSCF = 0.756 \exp[-(\log K_{ow} - 2.50)^2 / 2.58]$$

(9)

$$TSCF = 0.784 \exp[-(\log K_{ow} - 1.78)^2 / 2.44]$$

(5)

Recent reports have indicated that neutral, water-soluble chemicals with low hydrophobicities (log $K_{ow} < 1.5$) may still be taken up by rooted vascular plants in some cases. Aitchison et al. (21) showed that the heterocyclic ether 1,4-diozone is rapidly taken up and translocated by hybrid poplar cuttings. The TSCF was approximately 0.72, even though its log $K_{ow}$ is extremely low (−0.27), and it does not bind significantly to roots. It is suggested that chemicals such as 1,4-diozone and methyl-tert-buty ether (22) may be taken up via hydrogen bonding with water molecules into the transpiration stream.

**Enzymatic Transformations**

Phytotransformation refers to the uptake of organic contaminants from soil and groundwater and the subsequent metabolism or transformation by plants. Once an organic chemical is taken up and translocated, it undergoes one or more phases of transformation (11):

- **Phase I—Conversion:** oxidations, reductions, hydrolysis.
- **Phase II—Conjugation:** with glutathione, sugars, amino acids.
- **Phase III—Compartmentation:** Conjugates from phase II are converted to other conjugates and deposited in plant vacuoles or bound to cell wall and lignin.

Phase III conjugates are sometimes termed “bound residues” because of their inability to be extracted by chemical methods. These conjugates are likely covalently bound to stable tissues in the plant. However, one concern is whether under different conditions, such as in the gut of a worm or herbivore, there could be liganases or other enzymes able to sever covalent bonds and liberate the parent compound or toxic conjugate from the bound residue.

Chlorinated aliphatic compounds such as trichloroethylene (TCE) have been reported to be mineralized to CO$_2$ and less toxic aromatic metabolites (trichloroethanol, trichloroacetic acid, and dichloroacetic acid) by Newman et al. (3). These products are consistent with those found in the human liver for TCE destruction by cytochrome P450 (P450), which is an abundant enzyme in plants as well as humans (23). Thus, plants are sometimes viewed as “green livers” in terms of their enzyme biochemistry.

Nitrouridase and laccase enzymes in plants can break down ammouniation wastes such as 2,4,6-trinitrotoluene (TNT) and may incorporate the broken ring structures into new plant material or organic detritus that becomes a part of soil organic matter (2). Detoxification mechanisms may transform the parent chemical to nonphytotoxic metabolites stored in plant tissues. A thorough understanding of pathways and end products of enzymatic processes will simplify toxicity investigations of in situ phytoremediation.

**Phytotransformation**

**Enzymology and Biochemistry**

Plant degradation of many organic compounds follows pathways similar to those observed in other eukaryotes (24). Research on chlorinated aliphatic degradation in humans has focused mainly on their activation and resulting toxicity, carcinogenicity, or mutagenicity. The metabolism of these compounds can vary, even within a homologous series, but many go through oxidation to form a radical. This has been noted for carbon tetrachloride and to a lesser extent in other chlorinated methanes (28). The major dechlorination pathway for chlorinated ethylenes involves the formation of epoxides, with polychlorinated ethers such as TCE and tetrachloroethylene (PCE) alternatively being conjugated to glutathione (23). P450 is involved in epoxide formation, whereas glutathione S-transferase (GST) catalyses reactions with glutathione (23). TCE is one of the more studied compounds; metabolites commonly reported in experiments with rodents are chloral hydrate, trichloroethanol, dichloroacetic acid, and trichloroacetic acid (26). Transformation pathways of TCE in mammals are shown in Figure 3. The epoxide

| Chemical       | Log $K_{ow}$ | Solubility—log $C_{sat}$ | Henry’s Constant $K_{H}$, at 25°C (atmospheres) | Vapor pressure $P^*$ at 25°C (atmospheres) | TSCF | RCF (L/kg) |
|----------------|--------------|--------------------------|--------------------------------------------------|-------------------------------------------|------|-------------|
| Benzene        | 2.13         | 1.64                     | 0.2250                                            | 0.80                                      | 0.62 | 1           |
| Toluene        | 2.69         | 2.25                     | 0.2790                                            | 1.42                                      | 0.81 | 3           |
| Ethylbenzene   | 3.15         | 2.80                     | 0.3240                                            | 1.90                                      | 0.80 | 2           |
| m-Xylene       | 3.20         | 2.77                     | 0.2520                                            | 1.98                                      | 0.78 | 11          |
| TCE            | 2.33         | 2.04                     | 0.4370                                            | 1.01                                      | 0.75 | 3           |
| Aniline*       | 0.90         | 0.41                     | 2.2 × 10$^{-5}$                                    | 2.89                                      | 0.32 | 420         |
| Nitrobenzene   | 1.83         | 1.77                     | 0.0025$^a$                                        | 3.68                                      | 0.62 | 3           |
| Phenol*        | 1.45         | 0.20                     | >1.0 × 10$^{-5}$                                   | 3.59                                      | 0.48 | 11.6        |
| Pentachlorophenol | 5.04   | 4.27                     | 1.5 × 10$^{-5}$                                    | 6.75                                      | 0.04 | 30          |
| Atrazine       | 2.69         | 3.81                     | 1.0 × 10$^{-7}$                                    | 9.40                                      | 0.57 | 8           |
| 1,2-Trichlorobenzene | 4.25 | 3.85                     | 1.130                                              | 3.21                                      | 0.24 | 19          |
| 1,4-Dioxane    | –0.27        | Miscible                 | 2.0 × 10$^{-4}$                                    | 0.05                                      | 0.72 | <1          |
| Methyl-tert-butyl ether | 1.1 | 0.36                     | 0.56                                               | 0.49                                      | 0.65 | <1          |
| RDX            | 0.87         | 4.57                     | —                                                 | —                                         | 0.25 | 3.1         |

*aMeasured data from hydroponic studies with hybrid poplars. **Data from Burken and Schnoor (5), Lang (19), Althison et al. (27), and Winnike (22).<sup>1</sup>

* $K_{pK} = 4.87$, ** $K_{pK} = 9.99$. 

---

**Figure 3.** TCE metabolism in mammalian systems (23).
Dietz and Schnoor

intermediate is highly transient and difficult to detect. Thus, its role in the overall metabolism of TCE is still controversial and relatively uncertain.

Chlorinated ethanes are less studied, although the major metabolites reported in rat urine are trichloroethanol and trichloroacetic acid (27). Rats exposed to 1,1,1-trichloroethane (111TCA) by inhalation under hypoxia were found to exhale acetylene (28). Whereas chlorinated ethylenes are converted by P450 through an epoxide intermediate, ethanes go through chlorine or hydrogen abstraction, producing a free radical carbonium intermediate. In general, chlorinated ethylenes are more reactive than the ethane analogues. Potential transformation pathways for 111TCA are shown in Figure 4.

Phytotransformation has been studied most with pesticides in crop plants. These compounds undergo a series of metabolic processes. The first phase introduces functional groups such as –OH, –NH2, or –SH and can most with pesticides in crop plants. These are shown in Figure 4.

The second phase involves conjugation with β-glucoside, glutathione, or amino acids, resulting in soluble, polar compounds (31). Insoluble conjugates with cell wall components also form in plants. These can form through nonselective reactions with free radicals used in lignin synthesis or by more selective incorporation into hemicellulose (24). Insoluble conjugates are typically reported as bound residue because of difficulty in further characterization. Detoxification of herbicides in plants is attributed to conjugation with glutathione catalyzed by GST (32). Many herbicide safeners (chemicals applied before or in conjunction with herbicide application to protect crop species from herbicide damage) promote glutathione conjugation and detoxification by either increasing levels of glutathione or increasing activity of GST (33). Other enzymes that may be involved in phase II reactions include O- and N-glucosyltransferases and malonyltransferases (29).

The third phase of plant metabolism is compartmentation and storage. Unlike mammals, plants do not have a way to excrete unwanted compounds, so soluble metabolites are stored in the vacuole or as part of cell wall material. The transport of glutathione conjugates into the vacuole has been demonstrated in barley cell cultures (34). P450s are involved in both bacterial and eukaryotic transformation of chlorinated aliphatics (23,35). They also detoxify many pesticides in plants as part of phase I metabolism. Therefore, it is likely that plant transformation of chlorinated aliphatics is also mediated by a P450.

In plants, most P450s are membrane bound in microsomes such as plastids or endoplasmic reticulum (36). Several can be induced by light (37), whereas others are induced by plant stresses such as wounding, pathogens, or xenobiotic compounds (38). Xenobiotic induction of P450s in animal systems (such as birds and fish) has led to its use as an indicator of environmental contamination (39,40).

More than 50 reactions in plants are catalyzed by P450s (38), including both oxidative and reductive dehalogenation, as shown in Figure 5 (41). Reductive dehalogenation of polyhalomethanes has been demonstrated in several P450s, suggesting that this may be a general reactivity, especially under low oxygen conditions (42).

There are several potential mechanisms for the uptake and transformation of chlorinated aliphatics in a plant–soil system. These are summarized in Figure 6. Possible mechanisms include microbial transformation in the rhizosphere, uptake of the chemical and/or its metabolites into the roots, xylem transfer of the compounds to the leaves, volatilization from the leaves, foliar uptake of chemicals from the air, phloem transfer, and bound residue formation throughout the plant. All these mechanisms may prove important in phytoremediation of sites contaminated with chlorinated aliphatics.

Several researchers have studied the fate of TCE in plants, with varying amounts of phytovolatilization and phytotransformation reported (43). Many investigators have had difficulty isolating and identifying the metabolic products termed bound residue (44–46). However, Newman et al. (3) have reported TCE metabolism to trichloroethanol, trichloroacetic acid, and dichloroacetic acid in hybrid poplar. These results suggest that plant degradation of chlorinated aliphatics likely occurs by oxidative pathways similar to those of mammalian systems. Overall mass balances have been poor, indicating that other processes or further transformations may be occurring. Figure 7 shows a potential reaction sequence and binding of xenobiotics that may occur within cells.

Transgenic Plants

One of the most recent advances in phytoremediation is the development of genetically modified plants able to take up and degrade contaminants. With increased understanding of the enzymatic processes involved in plant tolerance and metabolism of xenobiotic chemicals, there is new potential for engineering plants with increased phytoremediation capabilities (47–49). This type of technology has already been used for several years in agricultural applications, such as Roundup Ready (Monsanto, St. Louis, MO)

Figure 4. Metabolism of 111TCA in mammalian systems.

A

\[
\begin{align*}
\text{R1} & \text{+ R2} \\
\text{OH} & \rightarrow \text{R1H + R2} \\
\text{HX} & \rightarrow \text{R1 + R2} \\
\text{R1H + R2} & \rightarrow \text{R1 + R2} \\
\end{align*}
\]

B

\[
\begin{align*}
\text{R1} & \text{+ R2} \\
\text{HX} & \rightarrow \text{R1H + R2} \\
\text{R1H + R2} & \rightarrow \text{R1 + R2} \\
\text{R1H + R2} & \rightarrow \text{R1 + R2} \\
\end{align*}
\]

Figure 5. Oxidative (A) and reductive (B) dehalogenation activity mediated by P450s (41).

Figure 6. Potential uptake and transformation pathways of TCE in a plant–soil phytoremediation system (49).

Figure 7. Likely cellular transport and metabolic processes in plants.
and 2,4,6-trinitrotoluene was achieved by commonly found in groundwater. Higher dibromide, another halogenated hydrocarbon formation in most phytoremediation applications. because there is no need for plant reproduc-

fertilization of genetically engineered plants acceptance of genetically modified organisms for field applications, assuming that public form, which is volatilized from the transgenic thereby increasing mercuric ion tolerance and into enzymatically degraded like organic contami-

nating properties such as rapid growth, deep root structures, or high water uptake. Higher tolerance to the explosives glycerol trinitrate and 2,4,6-trinitrotoluene was achieved by transgenic tobacco plants expressing a micro-

bial pentaerythritol tetranitrate reductase (53). Denitration of glycerol trinitrate was also more rapid and complete in the trans-

genic seedlings. Although metals cannot be enzymatically degraded like organic contami-

nants, genetic engineering may improve phytoremediation of heavy metals. Rugh and coworkers at the University of Georgia have transferred a bacterial mercuric ion reductase into Arabadopsis thaliana and yellow poplar, thereby increasing mercuric ion tolerance and conversion to the less toxic elemental mercury form, which is volatilized from the transgenic plants (54,55). These improvements have great potential for field applications, assuming that public acceptance of genetically modified organisms can be achieved. The potential for cross-

fertilization of genetically engineered plants to wild types in the environment would need to be addressed. Sterile clones could be used because there is no need for plant reproduc-

tion in most phytoremediation applications.

One major advantage of genetically engi-

neered plants is that specific enzymes for degradation of a contaminant could be trans-

ferrred to a plant species that is indigenous to an ecosystem or has other desirable remedia-

tion properties such as rapid growth, deep root structures, or high water uptake.

Toxicity Issues

The relationship between plant transformation of xenobiotics and phytotoxicity is not com-

pletely understood. In mammalian systems the activation of TCE through the epoxide intermediate produces its carcinogenicity. Similarly, some phytotransformations may cause plant toxicity if further enzymatic activity cannot successfully break down metabolites or sequester them.

The relative effects of the nine chlorinated solvents on hybrid poplar were compared by plotting the percent increase in cutting mass versus hydropnic exposure concentration (Figure 8). In general, cuttings tolerated higher concentrations of solvents with fewer chlorine atoms within a series of homologous ethanes or ethanes. The number of chlorine atoms was more closely related to growth reduction than was the arrangement of the chlorine atoms, as observed by comparing lines for the three isomers of dichloroethanes (cis-dichloroethane (cDCE), trans-

dichloroethene (tDCE), and 1,1-

dichloroethylene (11DCE)) and for two trichloroethanes (111TCA and 1,1,2-

trichloroethane (112TCA)). Ethanes cause zero growth at lower concentrations than do similarly chlorinated ethanes. The reason for these trends is not yet known. It is plausible that the more highly chlorinated compounds require more enzymatic steps to metabolize them. Epoxide intermediates potentially formed from chlorinated ethanes may be more difficult to further metabolize than the possible carbonan intermediates formed from chlorinated ethanes. Further research is needed to elucidate the relationship between phytotransformation and phytotoxicity.

Conclusions

Phytoremediation has been advanced in the last few years by increased understanding of the mechanisms of plant uptake and the various types of enzymatic metabolism that occur. Sorption and uptake constants such as the RCF and TSCF may help model plant uptake rates of various chemicals, allowing more accurate prediction of treatment times required for phytoremediation technology. Research into enzymatic transformation path-

ways will help determine the ultimate fate of chemicals in a plant remediation system. Recent studies with transgenic plants show that specific degradation capabilities may be added to plant species selected for other reasons. Further research into the biochemical processing of xenobiotic compounds will pro-

vide insight into phytotoxicity constraints, and genetic engineering may allow plants to tolerate higher concentrations of chemicals. This new knowledge will allow phytoremedi-

ation to be applied more widely and effectively.

REFERENCES AND NOTES

1. Anderson TA, Guthrie EA, Walton BT. Bioremediation in the rhizo-

sphere: plant roots and associated microbes clean contami-

nated soil. Environ Sci Technol 27:2620–2636 (1993).

2. Schnoor JL, Licht LA, McCuecheon SC, Wolfe NL, Carrithers LH. Phytoremediation of organic and nutrient contaminants. Environ Sci Technol 29:318A–323A (1995).

3. Newman LA, Strand SE, Cho N, Duffy J, Elean G, Rusza M, ShortleF BB, Wilmoth J, Heidem P, Gordon MP. Uptake and biotransformation of trichloroethylene by hybrid poplars. Environ Sci Technol 31:1062–1067 (1997).

4. Hughes JI, Shanks J, Vanderlinden M, Lauritzen J, Bhadra R. Transformation of TNT by aquatic plant plant tissue cul-

tures. Environ Sci Technol 31:266–271 (1997).

5. Burken JS, Schnoor JL. Predictive relationships for uptake of organic contaminants by hybrid poplar trees. Environ Sci Technol 32:3379–3385 (1998).

6. Thompson PL, Ramer LA, Schnoor JL. Uptake and transformation of TNT by hybrid poplar trees. Environ Sci Technol 32:970–980 (1998).

7. Reskin J, Enley BD, eds. Phytoremediation of Toxic Metals: Using Plants to Clean Up The Environment. New York: John Wiley & Sons, 2000.

8. Terry N, Banuelos G, eds. Phytoremediation of Contaminated Soil and Water: Boca Raton Lewis Publishers, 2000.

9. Briggs G, Bromilow RH, Evans AJA. Relationships between lipophicity and root uptake and translocation of non-ionised chemicals by barley. Pestle Sci 13:495–504 (1962).

10. Schmid M, Piemel N, Zinser, B, Hart V, Durst F, Wernck-

Reichart D. Xenobiotics: substrates and inhibitors of the plant cytochrome P450. Environ Sci Poli Res 4:229–234 (1997).

11. Dhanaka S, Ishmael H, Shiono N, Yamada T, Iwai H. Cytochrome P450 and other xenobiotic metabolising enzymes in plants. In: Pesticide Chemistry and Bioscience: the Food-Environment Challenge, Special Publication 233 (Brooks GT, Roberts TR, eds). Cambridge, UK: The Royal Society of Chemistry, 1999:259–264.

12. Wernck-Reichart D, Haen A, Didierjan L. Cytochromes P450 for engineering herbicide tolerance. Trends Plant Sci 5:116–123 (2000).

13. Kobil M, Harms H. Metabolism of Norfurance in different plant cell cultures and intact plants. Environ Toxicol Chem 19:1304–1310 (2000).

14. Shimp JL, Tracy JY, Davis LJ, Lee E, Huang W, Erickson LE, Schnoor JL. Beneficial effects of plants in the remediation of soil and groundwater contaminated with organic materials. Crit Rev Environ Sci Technol 23:41–77 (1993).

15. Burken JS, Schnoor JL. Phytoremediation: plant uptake of atrazine and role of root exudates. J Environ Eng 122:958–963 (1996).

16. Dushenko V, Kumar PIB, Monro H, Rasink J. Rhizolitization: the use of plants to remove heavy metals from aquatic streams: Environ Sci Technol 28:1239–1245 (1995).

17. Salt DE, Prince RC, Pickering L, Rasink J. Mechanisms of cad-

mium mobility and accumulation in Indian mustard. Plant Physiol 109:1427–1433 (1995).

18. Salt DE, Pickering L, Prince RC, Sieira D, Dushenko V, Smith BD, Rasink J. Metal accumulation by arable and wild cereal species. Environ Sci Technol 31:1636–1644 (1997).

19. Lang S. The Sorption of Substituted Benzenes to Hybrid Poplar Trees (MS Thesis). Iowa City, IA:University of Iowa, 1998.

20. Burken JS, Schnoor JL. Uptake and metabolism of atrazine by hybrid poplar trees. Environ Sci Technol 31:1399–1406 (1997).

21. Achordson EW, Kelly SL, Alvarez PJJ, Schnoor JL. Phytoremediation of 1,4-dioxane by hybrid poplar trees. Water Environ Res 72:313–321 (2000).

22. Winnike SK. Phytoremediation of Methyl-tert-Butyl Ether (MTBE) by Hybrid Poplar Trees (MS Thesis). Iowa City, IA:University of Iowa, 1998.

23. Heschler D. Science, occupational exposure limits, and regula-

tions: a case study on organochlorine solvents. Am Ind Hyg Assoc J 51:523–530 (1990).
Dietz and Schnoor

24. Lamoureux GI, Rusness DG. Xenobiotic conjugation in higher plants. In: Xenobiotic Conjugation Chemistry, ACS Symposium Series 209 (Paulson GD, Caldwell J, Hutson DH, Merr JJ, eds). Washington, DC:American Chemical Society, 1986;62–105.

25. Rauws R. Turning on carcinogenic research on several fronts reveals how humans metabolize cancer-causing substances. Chem Eng News 74:31–34 (1996).

26. Miller RE, Guengerich PF. Oxidation of trichloroethylene by liver microsomal cytochrome P-450: evidence for chloride migration in a transition state not involving trichloroethylene oxide. Biochemistry 21:1090–1097 (1982).

27. Kroschwitz J, ed. Encyclopedia of Chemical Technology, 4th Edition. New York:John Wiley & Sons, 1993.

28. Durk H, Poyser JL, Klessen F, Hectylan A. Acetylene, a mammalian metabolite of 1,1,1-trichloroethane. Biochim J 296:353–356 (1995).

29. Trapp S, McFarlane JC, eds. Plant Contamination: Modeling and Simulation of Organic Chemical Processes. Boca Raton, FL:Lewis Publishers, 1994.

30. Cole D. Oxidation of xenobiotics in plants. In: Progress in Pesticide Biochemistry and Toxicology, Vol 3 (Hutson DH, Roberts TR, eds). New York:John Wiley & Sons, 1983;199–248.

31. Mars K. The functions and regulation of glutathione S-transferases in plants. Annu Rev Plant Physiol Plant Mol Biol 47:127–158 (1996).

32. Lamoureux GL, Rusness DG, Schroder P, Rennenberg H. Chlorobimane. Plant Cell Environ 20:449–460 (1997).

33. Edwards R. Characterisation of glutathione transferases and glutathione peroxidases in pea (Pisum sativum). Physiol Plant 98:594–604 (1996).

34. Coleman JOD, Randall R, Blake-Kalff MMA. Detoxification of xenobiotics in plant cells by glutathione conjugation and vacuolar compartmentalization: a fluorescent assay using mono-chlorobimane. Plant Cell Environ 20:449–460 (1997).

35. Li S, Wackett LP. Reductive dehalogenation by cytochrome P450SAR1: substrate binding and catalysis. Biochemistry 32:9325–9329 (1993).

36. Chrispeels MJ. The endoplasmic reticulum. In: The Biochemistry of Plants: A Comprehensive Treatise (Tolbert NE, ed). New York:Academic Press, 1980;389–412.

37. Kim Y-S, Hara M, Ikebukuro K, Miyake J, Ohkawa H, Karube I. Photo-induced activation of cytochrome P450/reductase fusion enzyme coupled with spinach chloroplasts. Biotechnol Tech 10:717–720 (1996).

38. Bolwell GP, Bozkuz K, Zimmerman A. Plant cytochrome P450. Phytochemistry 37:1491–1506 (1994).

39. Bouchsweiler BJ, Weigert FE, Fett K. An ELISA assay for cytochrome P450IA1 in fish liver cells. Environ Toxicol Chem 15:592–596 (1996).

40. Ratner BA, Melanccon MJ, Cutter TW, Herholz RL, King KA, LeCaptain LJ, Spann JW, Woodin BR, Stegeman JJ. Biomonitoring environmental contamination with pipping black-crowned night heron embryos: induction of cytochrome P450. Environ Toxicol Chem 12:1719–1722 (1993).

41. Schuler MA. Plant cytochrome P450 monooxygenases. Crit Rev Plant Sci 15:235–284 (1996).

42. Halliker BA. Catalytic reactivities and structure/function relationships of cytochrome P450 enzymes. Phytochemistry 43:1–21 (1996).

43. Orchard BJ, Doucette WJ, Chard JK, Bugbee B. Uptake of trichloroethylene by hybrid poplar trees grown hydroponically in flow-through plant growth chambers. Environ Toxicol Chem 12:1593–1602 (1993).

44. Nenzung V, Wolfe L, Carreira L. Plant enzyme dechlorination of halogenated hydrocarbons in transgenic plants containing mammalian cytochrome P450 2E1. Proc Natl Acad Sci USA 97:6287–6291 (2000).

45. French CE, Rosser SJ, Davies GJ, Nicklin S, Bruce NC. Biodegradation of explosives by transgenic plants expressing pentaerythritol tetranitrate reductase. Nat Biotechnol 17:491–494 (1999).

46. Raskin I. Plant genetic engineering may help with environmental cleanup. Proc Natl Acad Sci U S A 93:3164–3166 (1996).

47. Hooker BS, Skene RS. Transgenic phytoremediation blato off the scene. Nat Biotechnol 17:428–428 (1999).

48. Padgett RR, Kalac KH, Delannay X, Re DB, LaValliee BJ, Timis CN, Rhodes WK, Otero Y, Barry GF, Eichholtz DA, et al. Development, identification, and characterization of a glyphosate-tolerant soybean line. Crop Sci 35:1451–1461 (1995).

49. Delannay X, Bauman TT, Beckley DH, Buettner MJ, Cabe HD, Defelice MS, Deering CW, Diedrich TJ, Griffin J, Hapood ES, et al. Yield evaluation of a glyphosate-tolerant soybean line after treatment with glyphosate. Crop Sci 35:1461–1467 (1995).

50. Doty SL, Shang TG, Wilson AM, Targen J, Westergreen AD, Newman LA, Strand SE, Gordon MP. Enhanced metabolism of halogenated hydrocarbons in transgenic plants containing mammalian cytochrome P450 2E1. Proc Natl Acad Sci USA 97:6287–6291 (2000).

51. Rugh CL, Wilde HD, Stack NM, Thompson OM, Summers AO, Meagher PB. Mercuric ion reduction and resistance in transgenic Arabidopsis thaliana plants expressing a modified bacterial mer gene. Proc Natl Acad Sci USA 93:3182–3187 (1996).

52. Doty SL, Shang TG, Wilson AM, Targen J, Westergreen AD, Newman LA, Strand SE, Gordon MP. Enhanced metabolism of halogenated hydrocarbons in transgenic plants containing mammalian cytochrome P450 2E1. Proc Natl Acad Sci USA 97:6287–6291 (2000).

53. French CE, Rosser SJ, Davies GJ, Nicklin S, Bruce NC. Biodegradation of explosives by transgenic plants expressing pentaerythritol tetranitrate reductase. Nat Biotechnol 17:491–494 (1999).

54. Hugh CA, Wildi HD, Stack NM, Thompson OM, Summers AO, Meagher PB. Mercuric ion reduction and resistance in transgenic Arabidopsis thaliana plants expressing a modified bacterial mer gene. Proc Natl Acad Sci USA 93:3182–3187 (1996).

55. Hugh CA, Seneff JF, Meagher PB, Merlo SA. Development of transgenic yellow poplar for mercury phytoremediation. Nat Biotechnol 16:525–528 (1998).