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**ECOLOGICAL EXPOSURE AND EFFECTS OF
AIRBORNE TOXIC CHEMICALS: AN OVERVIEW**

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16. ABSTRACT Since the release of the Environmental Protection Agency's (EPA's) toxic release inventory (TRI) estimates for 1987, there has been a heightened concern over the nation's air quality. Primarily, this concern has been directed at human health effects in industrial-urban areas. The fact that many airborne chemicals pose hazards to human health is only one aspect of the problem. The continued deposition of airborne toxic chemicals pose threats to both terrestrial and aquatic ecosystems, this discussion is limited to terrestrial vegetation.		
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EFFECTS OF ORGANIC CHEMICALS IN THE ATMOSPHERE ON TERRESTRIAL PLANTS

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INTRODUCTION

Thousands of organic compounds are released into the atmosphere each year by human activity. Of these, the U.S. Environmental Protection Agency (EPA) has classified 328 as Priority Pollutants, based on scientific evidence of toxicity in humans and other animals. However, only two, benzene and vinyl chloride, have National Ambient Air Quality Standards. Until recently, our knowledge of environmental releases of these substances was sketchy. In 1986, Congress passed the Emergency Planning and Community Right-to-Know Act, requiring manufacturers of Priority Pollutants to report the amounts of each that they released, deliberately or accidentally, into air, water, and soil. The results of the first round of the Toxic Release Inventory (TRI) revealed that 865,000 metric tons of toxic organic compounds were released to the atmosphere in 1987 (US EPA, 1989). Small manufacturers (<3,400 kg/year) and end users (e.g., farmers applying pesticides) were not required to report, and no attempt was made to incorporate emissions from area sources (dry cleaners, motor vehicle exhausts, etc.). Thus, total emissions were probably several times larger than the TRI data indicate.

Following emission, organics are dispersed widely in the environment. Long-distance transport occurs primarily in runoff, groundwater, and the atmosphere (Cohen, 1986). The latter pathway has spread organics to the most remote regions of the globe (Schroeder and Lane, 1988). Chlorinated pesticides such as DDT, lindane, dieldrin, and hexachlorobenzene (HCB) are the best-known examples, having been detected in inorganic media and organisms as distant from emissions

as the Arctic and Antarctic (Atlas and Giam, 1981; Tanabe et al., 1983; Gregor and Gummer, 1989). Long-distance dispersal of nonpesticide organics, including polycyclic aromatic hydrocarbons (PAHs), polychlorinated biphenyls (PCBs), chlorophenols, and alkanes, has also been demonstrated (Lunde and Bjorseth, 1977; Helt et al., 1984; Paasivirta et al., 1985; Wickstrom and Tolonen, 1987; Gregor and Gummer, 1989).

What are the consequences of this global organic contaminant load on the structure and function of organisms and natural ecosystems?

PROBLEM STATEMENT

A vast amount of literature has been accumulated on the ecotoxicology of organics in natural environments. However, it is quite clear that the driving force for research has been the concern over their accumulation in crops for human or livestock consumption, primarily as residues following pesticide applications, and in accumulation via biomagnification up aquatic and terrestrial food chains to organisms that are consumed by humans (e.g., fish), or organisms that bring us aesthetic pleasure (e.g., birds). There is, comparatively, a severe dearth of information concerning the fate and effects of toxic organics in noncrop, terrestrial, vascular plants.

The only comprehensive assessment of the literature on organic chemicals and terrestrial plants is the EPA-funded PHYTOTOX computer database (Fletcher et al., 1988). This database contains 77,825 dose-response (effects) records gleaned from 9,700 bibliographic references published between 1926 and 1984. Of the 1,569 species represented in PHYTOTOX, only 417 are native species growing in natural habitats. The latter value increases to 557 if old-field-succession species are included. Together, wild-grown and old-field species constitute 4,524 records, or 5.8% of the total database. Thus, the existing literature is heavily oriented toward agronomic species. Pesticides constitute 21% of all PHYTOTOX effects records. In fact, of the 20 most often cited chemicals, only two (both hormones) are not pesticides. And, only 4.7% of records are for native plants growing in natural environments.

From the toxicological standpoint alone, it is evident that insufficient data exist for EPA to undertake risk analyses for the effects of organics on natural terrestrial vegetation. In addition, little is known concerning deposition rates of organics to terrestrial ecosystems, rates of plant uptake, and subsequent translocation and metabolism.

The objectives of this report are to: (1) discuss mechanisms of atmospheric deposition of organic substances to terrestrial vegetation; (2) describe probable pathways of terrestrial vascular plant uptake of organics; (3) summarize existing literature on the effects of organics on terrestrial vascular plant growth and physiological processes; (4) speculate on potential, as yet unstudied, effects; and (5) recommend areas for future research.

I rely heavily on the herbicide literature, which greatly exceeds that for all other organics combined, but make no claim to provide any but the most cursory overview. I will consider all kinds of airborne organics, with the exceptions of peroxyacetyl nitrate (PAN), a known gaseous oxidant and phytotoxin that has received much attention during the last 20 years (see Mudd, 1975, for a review), and the chlorofluorocarbons. Also, I will not review the effects of water-borne organics on aquatic macrophytes.

CONCEPTUAL APPROACH

Figure 1 shows a model of the various fluxes of airborne organic substances onto, into, and through terrestrial vascular plants. Fluxes specific to the canopy are shown in detail in Figure 2. In the discussion that follows, I will deal with most of these fluxes, with the exception of within-soil fluxes, which are beyond the scope of this paper. Following that, I will describe known effects of organics on terrestrial plants, and finish with recommendations for future research.

ATMOSPHERIC DEPOSITION

Atmospheric Occurrence

Organics enter the atmosphere primarily in gaseous or particulate form. Initial mixing in the air leads to partitioning between the vapor, solid, and liquid phases (Schroeder and Lane, 1988). Phase distributions are determined by inherent chemical properties, including vapor pressures, Henry's Law constants (H , equilibrium ratio of the concentration in air to concentration in water), diffusion coefficients in air and water, and equilibrium constants (pK_a ; for weak acids) (Tucker and Preston, 1984; Mackay et al., 1986; Bidleman, 1988; Ligocki and Pankow, 1989). Organics enter precipitation by dissolving directly from the vapor phase into water droplets and by being physically scavenged as aerosols by falling droplets. The "washout ratio" (W ; mass of organics per unit volume of rain divided by mass of organics per unit volume of air) describes the net effect of these processes (Bidleman, 1988).

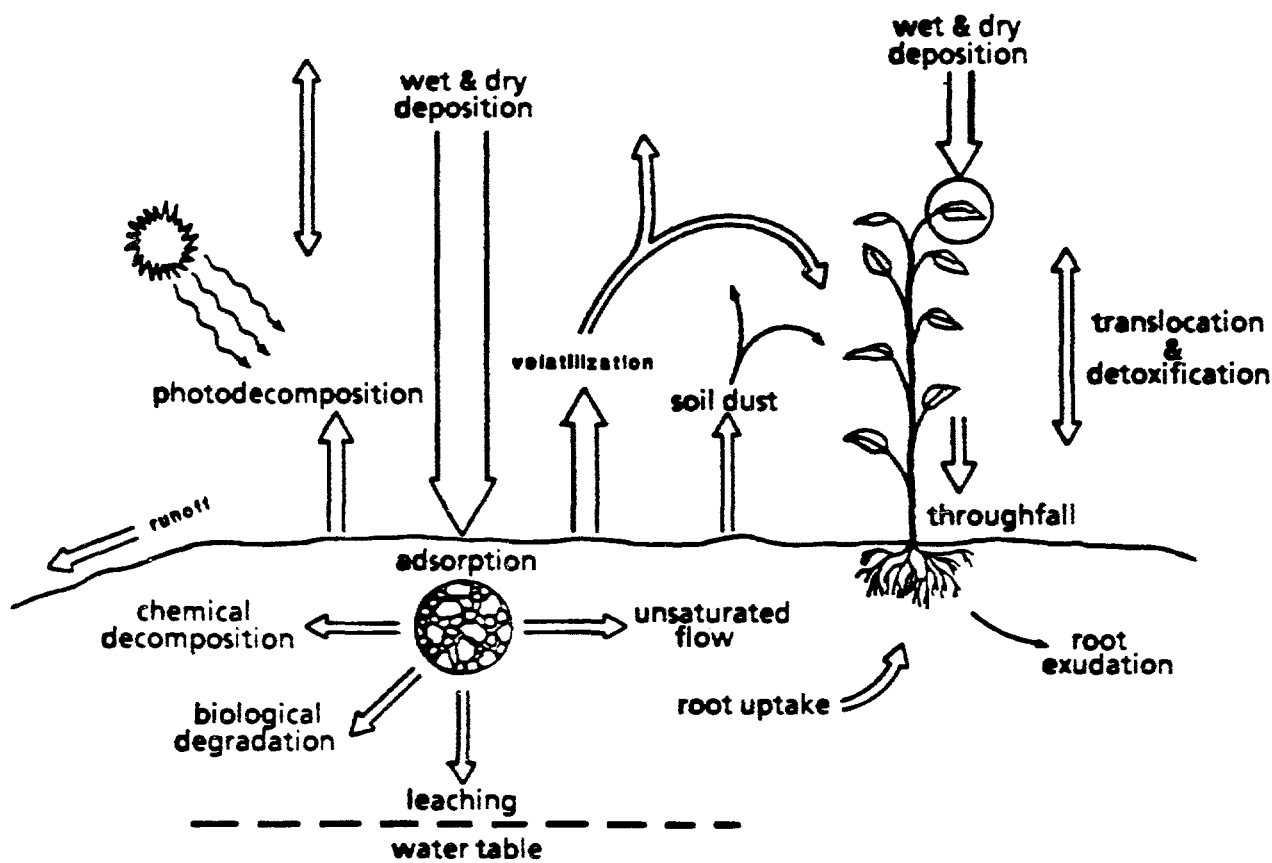


FIGURE 1. Conceptual model of fluxes of airborne organics to and within terrestrial ecosystems.

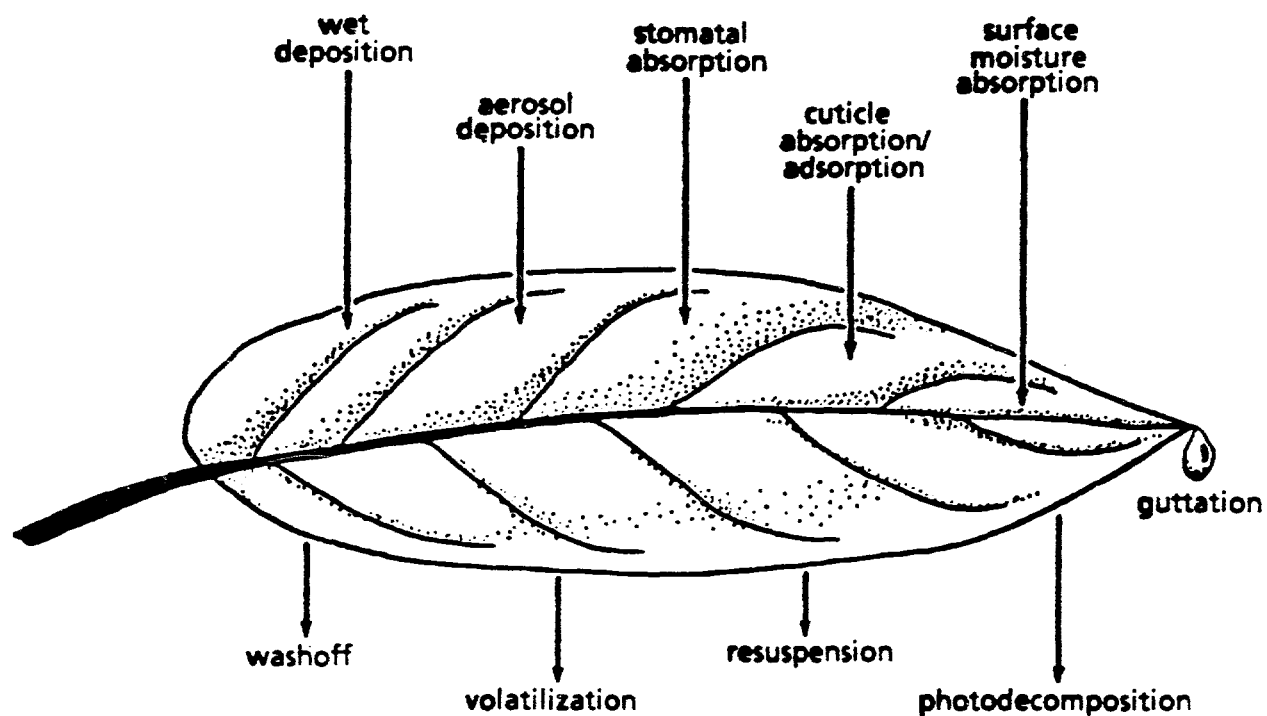


FIGURE 2. Same as Fig. 1, but enlarged to show fluxes associated with leaves.

Compared to the major air pollutants (ozone, sulfur dioxide, nitrogen dioxide, carbon monoxide), air concentrations of organics are not well-characterized. A great variety have been detected whenever and wherever they have been looked for. Urban air contains hundreds of volatile organic compounds (VOCs) from industrial emissions, motor vehicle exhausts, and other anthropogenic sources (Atlas and Giam, 1988; Bruckmann et al., 1988; Shah and Singh, 1988; Edgerton et al., 1989). Some VOCs are secondary products of the photochemical reactions that produce smog (e.g., nitrophenols [Nojima and Kanno, 1977]). These VOCs are transported downwind to rural regions (Rice et al., 1986; Rippen et al., 1987; Shah and Singh, 1988; Schroeder and Lane, 1988). Reverse transport also occurs; although having highest concentrations in agricultural areas, chlorinated pesticides are regularly found in urban air (Abbott et al., 1966; Stanley et al., 1971; Kaushik et al., 1987; Bruckmann et al., 1988). Natural vegetation, especially trees, puts out substantial quantities of VOCs, primarily monoterpenes, which mix with anthropogenic VOCs (Roberts et al., 1985; Trainer et al., 1987; Kreuzig et al., 1988; Petersson, 1988). Table 1 summarizes the range of concentrations of selected organics measured in air and rain.

TABLE 1. CONCENTRATIONS OF SOME PESTICIDES, PCBS, PAHS AND OTHER VOLATILE ORGANIC COMPOUNDS IN AIR AND WATER, UNITED STATES^a

Compound	Air (ng/m ³)	Rain (ng/L)
Hexachlorobenzene	0.13-0.29	0.40-1.0
α -/ γ -HCH	0.30-5.4	6.4-37
DDT/DDE	0.02-0.33	0.50-4.3
Chlordane	0.04-1.3	trace-2.3
Dieldrin	0.02-0.08	0.8-2.0
Toxaphene	0.6-13.1	7.31-59
PCBs	0.06-9.3	0.10-200
Phthalate esters	1.0-290	>200
Benzo(a)pyrene	1.3-500	2.2-7.3
Formaldehyde	2375-12250 ^b	<0.01-1.1
Acetaldehyde	0-9900 ^b	<0.04-1.1
Benzene	1950-10700 ^b	- ^c
Phenol	39-430 ^b	<10-14000
Benzo(a)pyrene	0.01-61	-

^a Sources: Pearson (1982), Nriagu and Simmons (1984), Giam et al. (1984), Chapman et al. (1986), Atlas and Giam (1988), Shah and Singh (1988), Leuenberger et al. (1988), Duinker and Bouchertall (1989), Sawicki et al. (1960)

^b lower/upper quartiles

^c no data available

Wet Deposition

The flux of organics to terrestrial ecosystems in precipitation is simply the volume-weighted product of the concentration in solution and precipitation volume, summed over the time period of interest. A growing literature reports concentrations of organic compounds in rain. Most regularly and widely detected are organic acids, especially aldehydes such as formate and acetate (Chapman et al., 1986 and references therein; Gaffney et al., 1987). Chlorinated pesticides, PCBs, phenols, and n-alkanes have all been reported in rain (Eisenreich et al., 1981; Farmer and Wade, 1986; Agarwal et al., 1987; Gaffney et al., 1987; Jones et al., 1989; Leuenberger et al., 1988; Atlas and Giam, 1988).

Few estimates of wet deposition flux for organics exist. Farmer and Wade (1986) observed 22 to 670 $\mu\text{g}/\text{m}^2/\text{day}$ for C_{12} - C_{32} hydrocarbon fluxes at Norfolk, VA. An estimate for bulk precipitation, which incorporates some aerosols, was 40 and 20 $\mu\text{g}/\text{m}^2/\text{y}$ for PCBs and lindane, respectively, at Paris, France (Chevreuil et al., 1989). Precipitation falling onto the Great Lakes has been analyzed for PCBs and pesticides for some years. Deposition rates are 0.6 to 9.6 $\mu\text{g}/\text{m}^2/\text{y}$ for chlorinated hydrocarbons, 424 $\mu\text{g}/\text{m}^2/\text{y}$ for PAHs, and 120 $\mu\text{g}/\text{m}^2/\text{y}$ for PCBs (Nriagu and Simmons, 1984).

Dry Deposition

Dry deposition of atmospheric substances onto natural vegetation is described by the equation

$$F = C_a * V_d$$

where F = flux density, C_a = atmospheric concentration at a reference height above the vegetation, and V_d = deposition velocity. Deposition velocity has four components:

$$V_d = 1/(r_a + r_b + r_s + r_c)$$

where r_a = bulk aerodynamic resistance, r_b = leaf or soil boundary layer resistance, r_s = stomatal resistance, and r_c = chemical resistance.

Aerodynamic resistance represents the turbulent downward movement of parcels of air, carrying entrained gases and particles. It is affected by wind speed, the surface area, and vertical distribution of canopy components (foliage, branches, etc.). Boundary layer resistances are related to wind speed and wind direction, and to collecting surface size and geometry. Stomatal resistance is

directly proportional to stomatal aperture, which is under physiological control by plants. Chemical resistance comes into play when the concentration of the compound at the absorbing surface is not zero (i.e., it is not quantitatively destroyed or sequestered upon deposition). In this case, the concentration gradient driving flux will be less than C_a .

Deposition of gaseous organics occurs primarily to dry soil and vegetation surfaces and is controlled largely by solubility in the waxy cuticles of plant surfaces and vapor-soil particle partitioning. Absorption of gaseous organics into water is important to wet soils, on plant surfaces following rain or during fog and dew events, in permanent wetlands, and in riparian areas during flooding. Deposition of organics in aerosol form is achieved by the same mechanisms as for aerosols in general: sedimentation, diffusion, and impaction. Sedimentation is most important for large aerosols, diffusion for small aerosols, and impaction for intermediate-sized aerosols (Garland et al., 1988).

Dry deposition of organics has been measured directly by accumulation on surrogate surfaces, including silicon oil-coated nylon screens (Sodergren, 1972); glass plates sprayed with mineral oil or water (McClure and Lagrange, 1977; Murphy, 1984); stainless steel funnels and sinks (Farmer and Wade, 1986; Chevreuil et al., 1989); and pans filled with water, ethylene glycol-water, or glycerin-water (Bidleman and Christensen, 1979; Christensen et al., 1979). Observed fluxes have been in the range 10^{-3} to $10^2 \mu\text{g}/\text{m}^2/\text{day}$ for PCBs and various pesticides, yielding V_d values of less than 0.01 to more than 5 cm/s. Confidence in these fluxes is not high because the efficiency collection of surrogate surfaces may vary substantially from that of natural surfaces. Bidleman and Christensen (1979) found that V_d for PCBs, chlordane, and DDT varied geographically and by one to two orders of magnitude from day-to-day. In addition, aerosol and gaseous deposition cannot be distinguished, and volatilization of adsorbed gases is not accounted for. Deposition velocities measured by accumulation have been used to infer dry deposition to the Great Lakes from known concentrations of organics in air (Eisenreich et al., 1981).

Fogs, Clouds, and Dew

Cloud water and fog water contain higher concentrations of organic acids and much higher concentrations of pesticides than does rain (Glottfelty et al., 1987; Igawa et al., 1989; Munger et al., 1989; Schaefer et al., 1989). Organic acids have also been reported from dew (Mulawa et al., 1986).

Interception of cloud water and of advective (seacoast) fog water is modeled as a dry deposition process, with cloud and fog droplets acting like large aerosols (Lovett, 1984). Deposition of radiation (valley) fog water is similar to precipitation (i.e., gravitational settling of water droplets). Dews form by condensation of water vapor onto surfaces whose temperature drops to the dewpoint;

deposition rates can be predicted using the Penman-Monteith equation. Organics enter dews by gaseous absorption and aerosol sedimentation. There appear to be no deposition estimates for organics in fogs, clouds, and dews.

Total Atmospheric Deposition

Accumulation rates of persistent (slow to degrade) organics in sediments yield an estimate of net atmospheric deposition (i.e., not accounting for volatilization). For example, Heit et al. (1981, 1988) and Gschwend and Hites (1981) measured PAHs in lacustrine and marine sediment cores in the northeastern United States. Fluxes in recent decades ranged from 36 to 4,870 $\mu\text{g}/\text{m}^2/\text{y}$, with greater fluxes near urban areas. Jones et al., (1989) measured PAHs in archived, dry soil samples collected since 1843 in rural England. Mean deposition rates (1880-1980) were 4,560 $\mu\text{g}/\text{m}^2/\text{y}$. Wickstrom and Tolonen (1987) found that PAH fluxes into sediments of small Finnish lakes had increased substantially since the early nineteenth century.

Swackhamer and Armstrong (1986) estimated net atmospheric deposition of 2 $\mu\text{g}/\text{m}^2/\text{y}$ of PCBs in recent decades to several small seepage lakes in Wisconsin. Rapaport and Eisenreich (1988) measured PCBs, HCB, DDT, and toxaphene accumulation in peat bog sediments. Maximum deposition rates in the eastern United States occurred between 1960 and 1978, with reduced rates since 1980.

The only estimate that could be found for recent atmospheric deposition of an organic to a terrestrial ecosystem was that of Matzner (1984) for German beech and spruce forests. Assuming no root uptake or exchange between surface deposits and canopy tissues, he estimated total PAH fluxes of 0.25 to 0.69 $\mu\text{g}/\text{m}^2/\text{y}$.

A regional application of mass balance was applied to the Great Lakes by the International Joint Commission (summarized in Elder et al., 1988). Measurements of PCBs and pesticide concentrations in dated sediments yielded values for long-term inputs. When known contributions of tributaries, runoff, and point sources were subtracted from these values, and outflows added, the difference was ascribable to atmospheric deposition. The atmosphere accounts for 60% of PCB inputs and 78% of benzo[a]pyrene inputs to the Great Lakes.

FLUXES OUTSIDE OF PLANTS

Fates in Soil

Once deposited, the disappearance of organics in soils usually follows first-order kinetics, provided no additional input occurs, and plant uptake is either constant or absent (Ryan et al., 1988). Factors contributing to the disappearance of organics include volatilization, photodecomposition, adsorption to soil particles, chemical and biological (microbial) degradation, unsaturated and saturated flow, and leaching to deeper soil layers (Figure 1). Consideration of these processes (except volatilization) is beyond the scope of this paper. However, modeling of disappearance rates is useful in determining the likelihood of organics to accumulate to concentrations at which plant root uptake will become significant (Ryan et al., 1988).

Volatilization

In general, volatilization rates of organics from plant canopies increase with increasing vapor pressures and decreasing Henry's law constants (H). Foliar volatilization rates do not fit simple first-order kinetics because of diurnal variability in environmental conditions (solar radiation, wind speed, etc.), and plant uptake (Willis et al., 1986). There is no simple relationship between volatilization rates of organics from soils and either vapor pressure or H values; such factors as adsorption coefficients to soil particles and soil moisture content are also important (Kilzer et al., 1979; Mackay et al., 1986; Spencer et al., 1988). Measured volatilization losses of herbicides in agricultural fields show great variability; 4.5% per year for dieldrin, but less than 1% per year for carbofuran (Caro et al., 1976); 80% per year for PCBs (Moza et al., 1979); 8, 24, and 34% over a six-day period for toxaphene, parathion, and fenvalerate, respectively (Willis et al., 1986); less than 1% over seven days for diclofop (Smith et al., 1986); and 21% over five days for 2,4-D (Grover et al., 1985).

A substantial proportion of herbicides volatilized from soils can be redeposited on crop canopies, especially DDT, PCBs, and the nitrophenol dinoseb (Parker, 1966; Prendeville, 1968; Beall and Nash, 1971; Kaufman, 1976; Moza et al., 1979; Fries and Marrow, 1981; Bacci and Gaggi, 1985). Topp et al. (1986) found that the proportion of soil-applied organic chemical uptake by barley foliage increased as the volatilized fraction of applied chemical increased.

Wash-Off and Resuspension

Wash-off occurs when rain physically dislodges particles or carries away dissolved gases and particulates from plant surfaces; these are then deposited to the soil in throughfall (Figures 1 and 2). The highest proportion of wash-off to amount applied is for pesticides with high solubility in water, for

those applied in particulate form, and when heavy or repeated rains occur shortly after application. Time-course studies of individual rain events reveal that wash-off is rapid at first, then diminishes asymptotically toward zero. Wash-off increases with increasing rain amount, up to some saturating intensity (Isensee and Jones, 1971; Steffens and Weineke, 1975; Cohen and Steinmetz, 1986; Willis et al., 1986).

Resuspension is the reentrainment of particles deposited on plant surfaces in moving air (Figure 2). Particle adhesion and windspeed are the primary factors influencing this process (Nicholson, 1988). Soil particles may be entrained in the atmosphere (wind erosion) or ejected into the air by raindrop splash (Chamberlain, 1975), from whence they may be redeposited on plant surfaces (Pinder and McLeod, 1988).

FLUXES INVOLVING PLANTS

Organics must penetrate plant tissues before they can exert physiological effects. Thus, aerosol deposition and nonstomatal deposition of gases are appropriately considered as separate processes from plant uptake. In the case of stomatal absorption, deposition and uptake are equivalent because the sink is the mesophyll.

Uptake rates are determined by external concentration, concentration in plant tissues, and resistances to uptake. For shoots, the most important physical barrier is the cuticle. For roots, the cell membranes of the endodermis are a significant barrier. Following uptake, if the substance is not translocated or metabolized to other forms, it may accumulate in tissues, reducing the concentration gradient across the plant surface, and thus reducing flux. Translocation to other parts of the plant, or metabolic conversion to other compounds, will lower internal concentration near the sites of uptake, maintaining the concentration gradient.

Foliar Uptake of Vapor-Phase Organics

Radioisotope studies with carbon-14 (^{14}C) labeled organics have demonstrated that in most plant species, uptake of PCBs is primarily by leaf vapor absorption, even when the PCBs are applied to the soil (Nash and Beall, 1970; Iwata and Gunther, 1976; Weber and Mrozek, 1979; Bacci and Gaggi, 1985). Nash and Beall (1970) and Beall and Nash (1971) found the same to be true of soybean plants exposed to soil-applied DDT, but soil volatilization was less important for dieldrin, aldrin, and heptachlor. PCBs accumulate in both herbaceous and woody species in proportion to PCB concentration in the surrounding atmosphere (Buckley, 1982). Soybeans absorbed ^{14}C -

anthracene vapors from air (Edwards et al., 1982). Accumulation of PCBs, DDT, penta-chlorophenol (PCP), nitrophenols, dioxins, furans, and α -hexachlorocyclohexane (α -HCH) also occurs in conifer foliage (Eriksson et al., 1989; Hinkel et al., 1989; Reischl et al., 1989a).

Gaseous hydrocarbons are readily absorbed by plant foliage. When tomato, barley, and carrot plants were exposed to hydrocarbon vapors (2×10^{-4} M), foliar damage symptoms appeared rapidly (Currier, 1951; Currier and Peoples, 1954). Frank and Frank (1989) exposed Norway spruce saplings to tetrachloroethene in glass chambers. The concentration of tetrachloroethene in the needles (C_n) increased linearly with increasing concentration in the chamber air. At $C_n < 5 \mu\text{g}/\text{cm}^3$, the partitioning between air and needles was greater than when $C_n > 10 \mu\text{g}/\text{cm}^3$, suggesting surface adsorption, followed by cuticular absorption when adsorption capacity was saturated.

Wolverton et al. (1984) reported that house plants absorbed formaldehyde from the air. However, additional experiments by Godish and Guindon (1989) established that the absorption was by potting soil rather than the plants. Bioconcentration of vapor-phase organics in leaves is closely correlated with their octanol-water partition coefficients [K_{ow} (Figure 3); Travis and Hattermer-Frey, 1988; Reischl et al., 1989b].

Foliar Uptake of Liquid-Phase Organics

Penetration of the cuticle by herbicides applied in solutions is positively related to their K_{ow} values (Shafer and Schonherr, 1985) and is usually linearly related to herbicide concentration (Bukovac, 1976). Uptake is generally greater to adaxial than to abaxial leaf surfaces, apparently because of the higher density of stomata and greater pubescence that occur on adaxial surfaces (Sargent and Blackman, 1962; Bukovac, 1976). Trichome bases and guard cells are preferred locations of uptake. Mass movement through stomata occurs if the organic, or its solvent, are lipophilic and have low surface tension (Baker, 1970; Bukovac, 1976). Most studies of foliar liquid uptake by herbicides, using ^{14}C labeling, have found substantial uptake (Bukovac, 1976; Steffens and Wieneke, 1975; van Auken and Hulse, 1979), but 2,4-dichlorophenol and dioxin do not appear to penetrate the cuticle (Isensee and Jones, 1971).

When Currier (1951) and Currier and Peoples (1954) exposed plants to pure hydrocarbon liquids, development of foliar damage was rapid, implying fast uptake across the cuticle. In a literature review on hydrocarbon oil effects on plants, Baker (1970) concluded that those oils containing mostly small-molecule, low-volatility hydrocarbons with low viscosity are most phytotoxic; the hydrocarbon constituents readily diffuse across cuticles and cell membranes, evaporative losses are low when applied to soils or foliage, and penetration through stomata occurs.

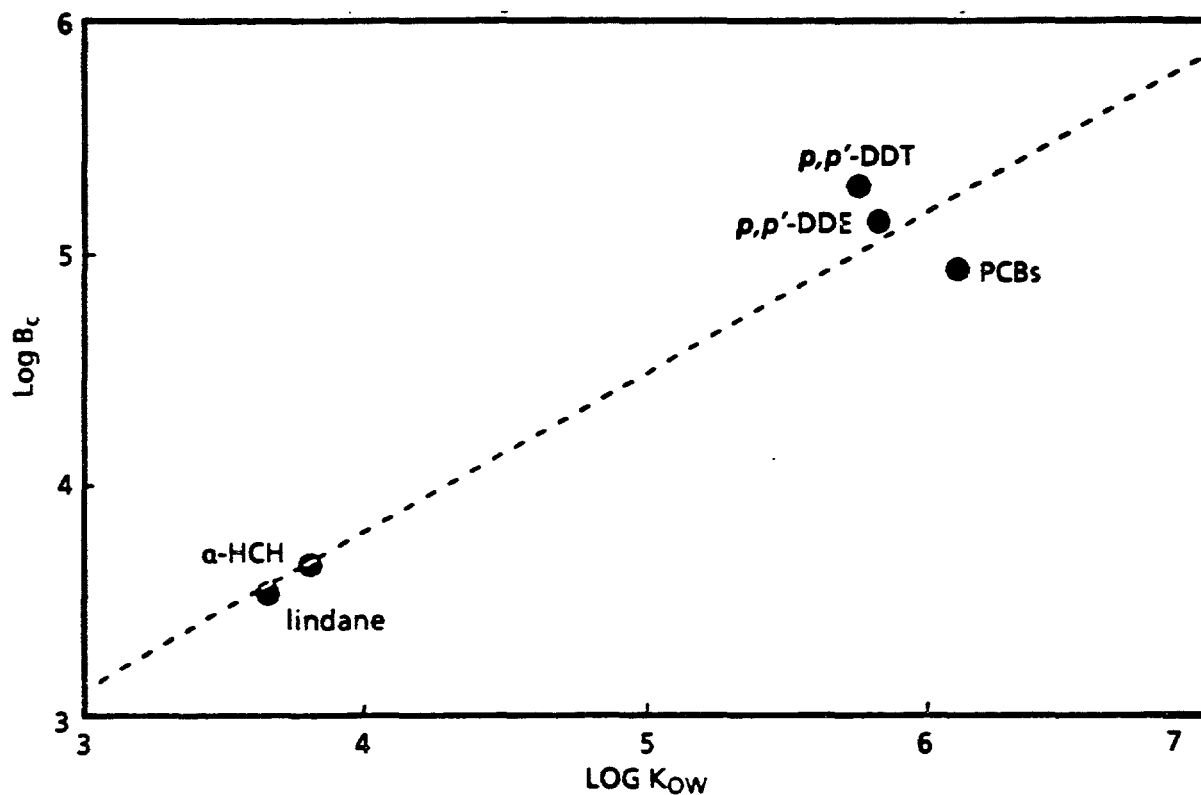


FIGURE 3. The relationship between bioconcentration of organics in plant tissues (B_c ; ratio of concentration in plant to concentration in air) and the octanol-water partition coefficient (K_{ow}) (after Travis and Hattermer-Frey, 1988).

Foliar Uptake of Solid-Phase Organics

Organics are frequently adsorbed to the surfaces of atmospheric aerosols, but no studies of particle-associated organic uptake by plants have been conducted. However, cuticular absorption of lipophilic organics is probably much faster from the vapor phase than from the solid phase (Reischl et al., 1989b).

Root Uptake

Many different herbicides are absorbed by the roots of crop plants (Lichtenstein and Schultz, 1965; Lichtenstein et al., 1967; Shone and Wood 1974; Bukovac 1976; Hilton et al., 1976; Briggs et al., 1982; Wickliff et al., 1984; McFarlane and Wickliff, 1985; Scheunert et al., 1986; Topp et al., 1986; McFarlane et al. 1987a,b). A linear relationship is often observed between soil or growth solution concentrations and rates of uptake, at least when concentrations are low. At higher concentrations, uptake may be saturated or even reduced (Fletcher et al., 1990), perhaps due to direct toxicity to the roots. If the original herbicide is not very soluble, root uptake rates may instead be related to concentrations of soluble soil metabolites (Scheunert et al., 1986).

Root uptake has been documented for the insecticides dieldrin, endrin, aldrin, and lindane, but does not occur for DDT and heptachlor (Harris and Sans, 1967; Lichtenstein et al., 1967; Nash et al., 1970). Root uptake has also been observed for dioxins, benzene and substituted benzenes, phenol and substituted phenols, ethanol, naphthol, acetate, tiaryl phosphate esters, phthalate esters, organo-borates, and trinitrotoluene (Harley and Beevers, 1963; Isensee and Jones, 1971; Kaufman, 1976; Suzuki et al., 1977; Moza et al., 1979; Mrozek and Leidy, 1981; Shea et al., 1982; Edwards, 1983, 1986; Casterline et al., 1985; McFarlane and Wickliff, 1985; Scheunert et al., 1985, 1986, 1989; Facchetti et al., 1986; Palazzo and Leggett, 1986; Sacchi et al., 1986; Topp et al., 1986; McFarlane et al., 1987a,b; Adriano et al., 1988; Aranda et al., 1989; Krstich and Schwarz, 1989; Fletcher et al., 1990; McFarlane et al., 1990; O'Connor et al., 1990). Depending on the species, plant roots may or may not absorb PCBs and PAHs (Edwards 1983, 1986; O'Connor et al., 1990).

During root uptake, organics move by diffusion in the apoplastic water of the cortex; then, at the Casparian strip, cross the cell membranes of the endodermis to reach the xylem. Shone and Wood (1974), Briggs et al. (1982, 1983), Topp et al. (1986), and McCrady et al. (1987) found a positive, log-linear relationship between the root concentration factor (RCF; ratio of root tissue concentration to external solution concentration) and K_{ow} for various organics. However, in a comparison of nitrobenzene absorption by eight plant species, RCF varied considerably around the

predicted value from Briggs et al. (1982), emphasizing the importance of species-specific characteristics (McFarlane et al., 1990).

Bark Uptake

Penetration of the bark of woody plants by herbicides has been reported (Bukovac, 1976). Meredith and Hites (1987) found a variety of PCB congeners in the bark of black walnut and tulip-poplar trees growing near a PCB-contaminated landfill. Very low PCB concentrations in the wood, much higher PCB concentrations in inner than in outer bark, and a positive correlation between congener K_{ow} and accumulation in outer bark suggested that uptake occurred from the atmosphere into the suberin of cork cells.

Translocation

When ^{14}C -labeled herbicides are taken up by roots, most move upward in the transpiration stream, but some remain in the cortex, apparently unable to cross the endodermis (Hay, 1976; Hilton et al., 1976). The proportion translocated varies according to length of exposure, plant species, and type of herbicide (McFarlane et al., 1987b). What is translocated may be found fairly uniformly in all the leaves or may be concentrated in young leaves and growing tips (Hay, 1976). Dry soils reduce rates of translocation, presumably due to lesser transpiration and a lower carbohydrate supply for phloem transport.

Translocation of root-absorbed, non-herbicide organics has been demonstrated for aldrin, lindane, bromacil, triaryl phosphate esters, phenol and chlorophenols, dioxins, phthalate esters, PCBs, trinitrotoluene, and nitrobenzenes (Lichtenstein et al., 1967; Isensee and Jones, 1971; Mrozek and Leigy, 1981; Shea et al., 1982; Casterline et al., 1985; Edwards, 1986; Palazzo and Leggett, 1986; Sacchi et al., 1986; McFarlane et al., 1987a,b, 1990; Aranda et al., 1989; Fletcher et al., 1990). Root- and leaf-absorbed hydrocarbon oils are transported acropetally and basipetally, respectively (Buckley, 1982). However, there is little translocation of root-absorbed PCBs, PAHs, and substituted phenols (Hilton et al., 1976; Kaufman, 1976; Dörr, 1970; Buckley, 1982; Scheunert et al., 1989), nor do root- or leaf-absorbed dioxins and furans appear to be translocated (Reischl et al., 1989b).

There is considerable evidence for a positive relationship between transpiration rate and root uptake (see Figure 4) (Bukovac, 1976; van Oorschot, 1976; McFarlane et al., 1987b). However, Shone and Wood (1976) discovered that neither external concentration nor transpiration rate had much effect on uptake and translocation of triazine herbicides by radish.

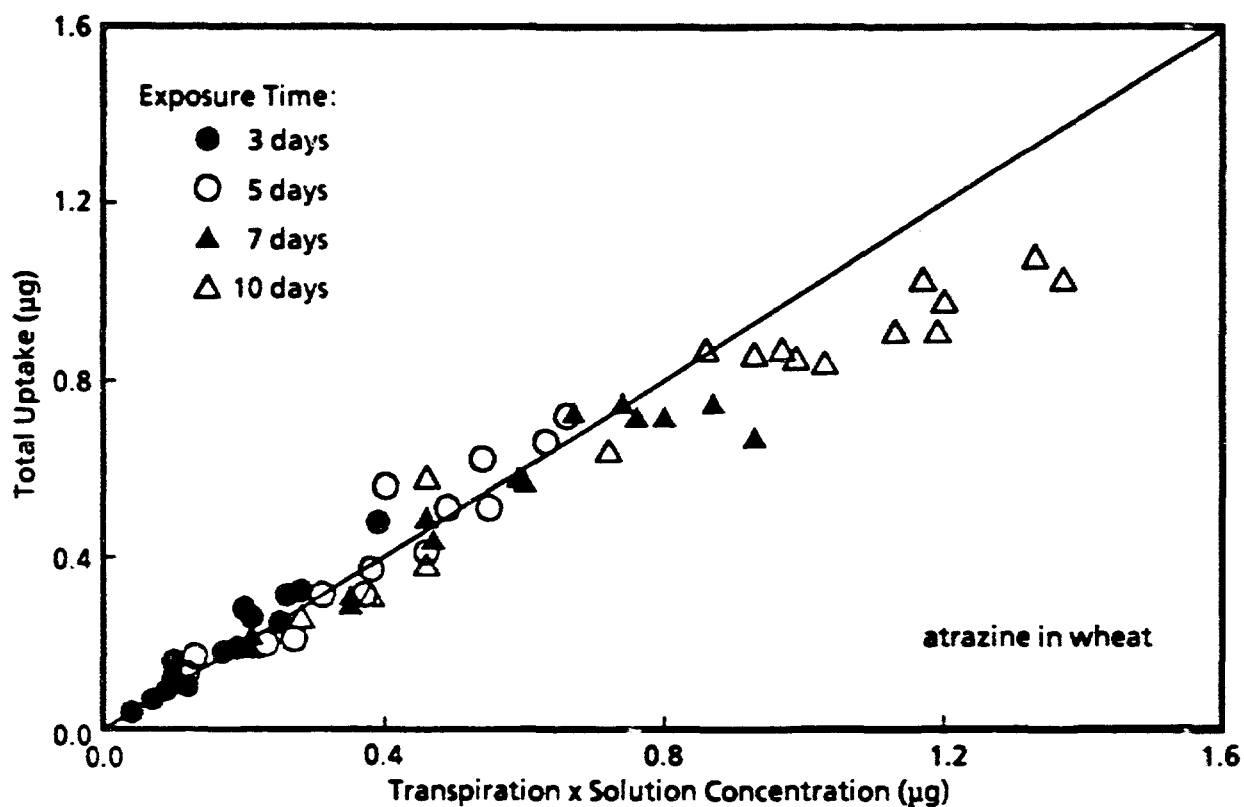


FIGURE 4. The relationship between total uptake of atrazine from solution by wheat and the expected uptake by mass flow through the xylem (after Walker, 1972).

Briggs et al. (1983) observed a positive, log-linear relationship between stem concentration factor (SCF; calculated in same way as RCF) and herbicide K_{ow} . It required 24 to 48 h for SCF to stabilize, with longer equilibration times for higher K_{ow} . They postulated that stable SCF represented abalance between upward transport of root-absorbed compounds and their absorption or degradation by stem tissues.

The herbicide transpiration stream concentration factor (TSCF; ratio of concentration in transpiration stream to concentration in external solution) in barley plants was usually less than unity, implying passive uptake of most herbicides, but greater than unity for 2,4-D, implying active uptake (Shone et al., 1973; Shone and Wood, 1974). The nitrobenzene TSCF was consistently less than one in eight plant species (McFarlane et al., 1990). The TSCF was not related in any obvious way to RCF. However, Shone et al. (1974) demonstrated that the TSCF was correlated with the most readily diffusible herbicide fraction in barley roots eluted with water following a period of root uptake. This fraction consisted of the most lipophilic (high K_{ow}) herbicides.

Briggs et al. (1982) observed a bell-shaped relationship between TSCF and K_{ow} in barley (Figure 5). They hypothesized that for $K_{ow} < 1.8$, transport is limited by diffusion across the endodermal membrane; whereas, for $K_{ow} > 1.8$, transport is limited by the rate of transport from the roots to the tops. McCrady et al. (1987) demonstrated that sorption to the xylem tissue was the main limitation on transport rates of organics through excised soybean stems. McFarlane et al. (1987b) found differential root uptake and translocation to the shoot of soybean by bromacil, nitrobenzene, and phenol, although the three chemicals have similar K_{ow} values. Given the scatter in Briggs et al. (1982) relationship, this result is not surprising. Boersma et al. (1988) have developed a model of organic compound transport in the xylem and phloem. This model is most sensitive to K_{ow} , rates of detoxification, membrane permeability, and the volume of xylem and phloem in various organs.

Generally, the bulk of foliar-applied organics is not translocated; that portion that is partitioned to the stem, little goes to the roots (Hay, 1976; Shone and Wood, 1976; Weber and Mrozek, 1979). Foliar-applied ureas, triazines, DNOC, PCP, and hexachlorophene are not translocated (Fogg, 1948; Hay, 1976; Kaufman, 1976; van Auken and Hulse, 1979).

Detoxification

Plants detoxify herbicides primarily by metabolic degradation and to a lesser extent by adsorption to biomolecules. Adsorption to lecithin and cell membranes has been demonstrated for 2,4-D and 2,4,5-T (Wain and Smith, 1976). The metabolic fates of many different herbicides have been elucidated by ^{14}C labeling studies (Naylor, 1976). In most cases, metabolism converts the

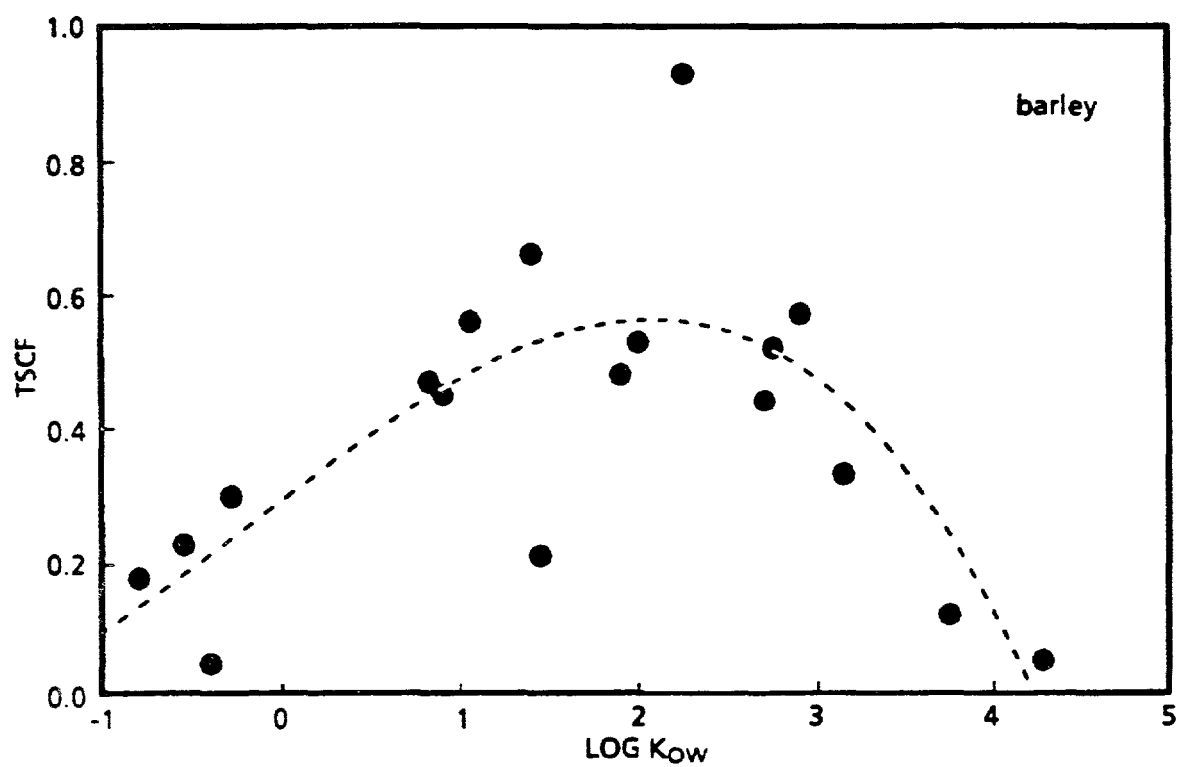


FIGURE 5. The relationship between transpiration stream concentration factor (TSCF; ratio of concentration in transpiration stream:concentration in nutrient solution) of various organics and octanol-water partition coefficients (K_{ow}) in barley (after Briggs et al., 1982).

phytotoxic herbicide to nonphytotoxic or less phytotoxic forms; however, the reverse is sometimes true (e.g., amitrole, bipyridyliums, 2,4-D precursors, DNOC esters) (Wain and Smith, 1976; Menn and Still, 1977). Generally, detoxification proceeds in two steps: (1) an oxidizing, reducing, or hydrolyzing reaction that modifies the organic toxin by adding reactive groups; and (2) a subsequent conjugation reaction that further reduces toxicity and yields a metabolite in a form suitable for storage or transport (Kaufman, 1976; Menn and Still, 1977).

The metabolic fates of most nonherbicide organics in plants are not well understood. Degradation of PAHs, phthalate esters, 4-nitrophenol dichlorobiphenyls, nitrobenzenes and trinitrotoluene have been reported (Dörr, 1970; Moza et al., 1979; Edwards, 1986; Palazzo and Leggett, 1986; McFarlane et al., 1987a, 1990; Fletcher et al., 1990; Preiss et al., 1989; Schmitzer et al., 1988), but the phytotoxicity of the metabolites is unknown.

One major mechanism of plant detoxification of organics is conjugation to glutathione. For example, corn, sorghum, and sugarcane, which possess this metabolic capability, resist atrazine; whereas broadleaf weeds and grasses, which do not have this capability, are susceptible to atrazine. Schroder and Rennenberg (1989) reported glutathione conjugation of pentachloronitrobenzene (often sprayed on crops to protect them from pathogens), but not of atrazine, by Norway spruce.

Plant Efflux

Efflux of organics from plants occurs in three ways: (1) foliar efflux or "leaching," (2) passive loss by transpiration, and (3) root exudation (Rovira, 1969; Tukey, 1970). Radiocarbon studies have shown that root exudation of herbicides is an energy-requiring process, occurs in the zone of active root elongation, and involves readily translocatable and little-metabolized herbicides (Bukovac, 1976). The extent to which organics taken up by plants may be subsequently lost by foliar efflux apparently has not been studied.

Siddaramappa and Watanabe (1979) exposed rice plants to ^{14}C -carbofuran in nutrient solutions sealed at the root collar to prevent volatilized carbofuran from reaching the leaves. Transpired carbofuran was trapped in ethylene glycol in shoot chambers. Over a 10-day period, 9 to 17% of the absorbed radioactivity was lost via transpiration, apparently carbofuran was carried passively along in xylem water. Higher transpiration rates resulted in more carbofuran recovered from the air. These authors also found significant radioactivity in guttation water. McFarlane et al. (1990) found that 10-40% of not-absorbed ^{14}C -nitrobenzene volatilized from leaves of crops and woody plants.

KNOWN EFFECTS ON PLANTS

Visual Injury and Growth

As with plant uptake, there is a close association between K_{ow} values of organics and their inhibitory effects on plant germination and growth. A good model that fits a wide range of plant data is a nonlinear equation where toxicity increases linearly up to a critical value of K_{ow} , then falls off at higher K_{ow} (Hansch et al., 1989).

Herbicides

The mechanisms by which herbicides influence growth include inhibition of mitosis, inhibition or stimulation of tissue enlargement and elongation, and alteration of patterns of tissue differentiation (Cartwright, 1976). Herbicides may also alter dry mass distribution among plant organs, prevent pollination, and cause abscission of leaves and other plant parts (Addicott, 1976; Ratsch et al., 1986); and, in the case of auxin-like herbicides such as 2,4-D, abnormal growth of various organs (van Andel et al., 1976). Effects may be manifested at all stages of growth from germination to reproduction. For example, Sund and Nomura (1963) observed that some herbicides were most effective in inhibiting germination, others at inhibiting seedling growth, and still others at inhibiting growth of juvenile plants. Several herbicides, including dinoseb, PCP, 2,4-D and 2,4,5-T were inhibitory at two or more of these life stages.

Substituted phenols vary widely in their effects on germination and seedling growth (Sund and Nomura, 1963; Amer and Ali, 1968; Shea et al., 1983). Root growth is stimulated by 2,4-dinitrophenol (DNP) at low concentrations and is inhibited at high concentrations, probably because it is a respiratory uncoupler (Shea et al., 1983). Chlorosis, wilting, and necrosis of peas is caused by 2-nitrophenol and 2,4-dichlorophenol (Amer and Ali, 1968).

Van Haut and Prinz (1979) studied the effects of a number of organic vapors on the growth of several crop species. Over a wide range of concentrations ($0.1-7.0 \text{ mg m}^{-3}$), relative growth reductions were positive log-linear for all chemicals and species studied. Growth reductions relative to those caused by sulfur dioxide at equivalent concentrations varied between plant species and were usually higher at lower concentrations. The most phytotoxic substance was ethylene (up to eight times the growth reduction of sulfur dioxide), followed by formaldehyde and acetic acid. Dimethylformamide and methanol were less phytotoxic than sulfur dioxide. Dichloromethane, toluene, trichloroethylene, acetone, and xylene caused little or no growth reduction at concentrations up to $60-160 \text{ mg/m}^3$.

Surfactants are often used to improve "wettability" of foliar-applied herbicides. These substances may in themselves increase, reduce, or have no effect on the growth of crops (Lichtenstein et al., 1967; Singh and Orsenigo, 1984).

Other Organics

Toxicity of pure hydrocarbon sprays applied to plants increases in the order: straight-chain paraffins < naphthenes and alkenes < aromatics (Crafts and Reiber, 1948). When barley, tomatoes, and carrots were exposed to hydrocarbon vapors, toxicity increased in the order: benzene < toluene < xylene < trimethylbenzene (Currier, 1951). The symptoms started with increased foliage odor, followed by the appearance of dark areas on the foliage, wilting, and, at higher concentrations, death. Shoot dry mass gain was positively correlated with vapor concentration for sublethal doses. When these same compounds were sprayed on foliage as pure liquids, the same order of toxicity was observed, but the differences among hydrocarbons were greater, apparently because of differences in volatilization (vapor pressure decreasing in reverse order to toxicity). Currier and Peoples (1954) repeated these experiments, finding that toxicity increased in the order: hexene < hexane < cyclohexane < cyclohexene < benzene.

Crude oils, their refined products, and coal liquid cause visual injury and reduce growth of a variety of weed and crop species (Baker, 1970; Blankenship and Larson, 1978; Warner et al., 1984). Toxicity is due to the mixture of hydrocarbons in these liquids, including alkanes, alkenes, naphthenes, naphthalenes, phenols, and aromatics. Many hydrocarbons are known to be toxic in the presence of ultraviolet radiation (Larson and Berenbaum, 1988). For example, the PAH fluoranthene causes foliar injury under UV light (Zweig and Nachtigall, 1975). Creosote, a widely used wood preservative, contains a variety of PAHs and other aromatics. Concentrations of 18 to 34 mg/L reduced root growth of onion by 50% (Sundstrom et al., 1986).

Aroclor 1254, a mixture of PCBs, inhibited height growth and fresh mass increase of both soybean shoots and roots; at higher concentrations, newly formed leaves showed abnormal curling (Weber and Mrozek, 1979). Phthalate esters caused reduced growth and chlorosis of new leaves and growing tips of tobacco and corn (Buta, 1975; Shea et al., 1982). Tributyl phosphate reduced root growth of rice, radish, and soybean at concentrations of 10 to 100 $\mu\text{g/g}$ soil (Muir, 1984). Trinitrotoluene (TNT) lowered root and shoot growth of nutsedge (Palazzo and Leggett, 1986). Sodium tetraphenylborate (NaTPB) reduced growth of loblolly pine seedlings because of increased plant boron uptake to toxic levels (Kaplan et al., 1988). NaTPB's major degradation product, diphenylboric acid (DPBA), did not affect growth. However, both NaTPB and DPBA, as well as biphenyl, another breakdown product, reduced growth of sorghum, with NaTPB having the greater influence (Adriano et al., 1988).

Many substituted phenols have auxin-like activity. Harper and Wain (1969) found that the greatest growth promotion in standard auxin activity tests was produced by phenols with substitution at both ortho-positions. Like phenols, PAHs can stimulate plant growth (Gräf and Nowak, 1966). Several alcohols promoted growth of excised wheat roots in the light, whereas others had no effect (Gudjonsdottir and Burstrom, 1962). Hexadecanol and docosanol decreased growth of tobacco (Bourget and Parups, 1963). Organic acids and aromatic alcohols, aldehydes, and carboxylic acids inhibited lettuce germination (Mayer and Evenari, 1953; Reynolds, 1978). The insecticides parathion, diazinon, and lindane significantly reduced root growth, but not shoot growth, of peas; whereas, simazine reduced both root and shoot growth (Lichtenstein et al., 1967). Vapor-phase aldehydes at concentrations > 0.2 ppm caused foliar injury to petunias (Brennan et al., 1964).

Gas Exchange and Water Relations

Herbicides

For most herbicides studied to date, stimulation, inhibition, or no effect on dark respiration have been reported (van Oorschot, 1976). In some cases, lower concentrations stimulate; whereas, higher concentrations inhibit, a typical response for oxidative uncouplers such as DNP (Shea et al., 1983). Respiration may also be affected differentially by the same herbicide in different plant organs.

Inhibition of net photosynthesis has been observed in a wide variety of herbicides when plants are exposed to herbicides in soils or nutrient solutions, or applied to foliage (van Oorschot, 1976). With the exception of acylamides, virtually all herbicides tested to date inhibit net photosynthesis and, when a range of concentrations is studied, inhibition increases with increasing concentration. Unlike respiration, stimulation of net photosynthesis has not been observed (van Oorschot, 1976).

All herbicides that reduce net photosynthesis reduce transpiration as well, such as DNP (Barber and Koontz, 1963; Pemadesa and Korelege, 1977). This phenomenon raises the question as to whether or not photosynthetic inhibition is primarily due to stomatal closure, or to nonstomatal (biochemical) effects. Nonstomatal inhibition can be represented as a "mesophyll resistance" (r_m) in series with r_b and r_s . Imbamba and Moss (1971) found that r_m for CO_2 in corn exposed to atrazine increased without an accompanying change in r_s . Most evidence for the relative roles of r_s vs. r_m is indirect, however. When photosynthesis and transpiration were measured simultaneously following exposure to ureas, triazines, diazines, bipyridyliums, and simeton, the relative reduction in photosynthesis was greater than that of transpiration, and commenced sooner (van Oorschot, 1976). This suggested direct herbicidal action at the sites of photosynthesis. However, for PMA, DSA, loxynil, propanil, nitrofen, and fluorodifen, photosynthesis and transpiration were inhibited to a similar extent and at the same time, implying that stomatal closure restricted uptake of CO_2 . Similar

variations in the relative reduction of transpiration vs. ~~photosynthesis~~ were observed for nitrobenzene (McFarlane et al., 1990). Herbicides also disrupt the water economy of plants by reductions in root water uptake, as reported for phenoxy herbicides, ureas, triazines, propanil, and dinoseb (van Oorschot, 1976).

Herbicides that inhibit the light reactions of photosynthesis often inhibit photorespiration as well. This has been demonstrated by similar reductions in net photosynthesis of wheat and corn in air with normal and low O₂ concentrations following exposure to diuron (Downton and Tregunna, 1968), and by the absence of the postillumination CO₂ burst in barley exposed to atrazine (Imbamba and Moss, 1971). However, when corn was exposed to atrazine, CO₂ evolution in the light was greater than in darkness, suggesting little or no suppression of photorespiration (van Oorschot, 1976).

Other Organics

Organic chemicals other than herbicides have been shown to influence plant growth and development. Wood et al. (1985) and Wood and Payne (1986) found that pecan leaves sprayed with the fungicides propiconazole, benomyl, triphenyltin hydroxide, and dodine, or with pyrethroid, carbamate, and organophosphate insecticides showed inhibition of net photosynthesis of up to 20% within one day following application, with full recovery usually occurring within several days. Hydrocarbon oils universally reduce transpiration and net photosynthesis of crops (Baker, 1970). Recovery of both processes is correlated with the dissipation of foliar-applied oils, and raising the CO₂ concentration of the air reduces inhibition, suggesting that blockage of stomata is the cause of inhibition. However, due to the rapidity with which hydrocarbons penetrate leaf tissues, nonstomatal effects are likely as well. Hydrocarbon oils either increase or decrease respiration, with the effect differing among oils and between plant species (Baker, 1970). Nitrobenzene at 8 g/L in growth solution had varying effects on gas exchange of several species; ranging from no effects on soybean to complete photosynthetic repression of green ash (McFarlane et al., 1990). Even at 100 g/L, nitrobenzene did not affect soybean gas exchange (Fletcher et al., 1990).

One hypothesis to account for European forest-tree decline or "Waldsterben" is phytotoxicity of anthropogenic and biogenic hydrocarbons. When young Norway spruce were exposed to β -pinene vapors, photosynthesis was inhibited and chlorophyll degraded (Gross et al., 1988; Wagner et al., 1989). β -pinene inhibits the Hill reaction (Pauly, 1981), resulting in uncoupling of oxidative phosphorylation (Wagner et al., 1989). Frank and Frank (1985) were able to reproduce the decline symptom of needle yellowing in Norway spruce by exposing branches to vapors of two anthropogenic VOCs, tri- and tetrachloroethene, in the field. They later showed (1986, 1989) that these compounds were absorbed by spruce needles and, in the presence of sunlight, the compounds caused photodegradation of photosynthetic pigments. Rippen et al. (1987) have speculated that nitrophenols injure forests.

Ultrastructure and Membrane Function

Because most organics are lipophilic, it is not surprising that they often disrupt cell membranes. At low concentrations, dissolution of organic molecules in membranes forces apart the fatty acid chains of the phospholipids, increasing membrane permeability. At higher concentrations, the bilayer configuration may disintegrate completely. Some organics disrupt cell membranes indirectly through the formation of free radicals, inhibition of lipid synthesis, or changes in the types of lipids synthesized. The disruption of membranes probably accounts for many of the ultrastructural changes attributed to organics.

Herbicides

Contact foliar damage ("burning" or "wetness") by 2,4-D, endothal, and several other herbicides is believed to result from physical disruption of cell membranes (Morrod, 1976). Paraquat disrupts membranes because its metabolism produces hydrogen peroxide (Morrod, 1976). Two consequences of membrane damage are leakage of cell contents and altered rates of active uptake. For example, DNP increases plant cell permeability to water, whereas stomatal closure caused by atrazine, 2,4-D, and DNP may be caused by leakage of K^+ from guard cells (Morrod, 1976; Shea et al., 1983). Ultrastructural changes induced by herbicides in leaves include swelling of thylakoids and chloroplasts, destruction of phloem and vascular cambium, abnormal differentiation of xylem, bark, and root cells, and mitotic abnormalities (Amer and Ali, 1969; Linck, 1976; Moreland and Hilton, 1976).

Other organics

Despite rather low K_{ow} values, bulky hydrocarbons are effective at disrupting membranes. For example, heptene-2, with a bent configuration, causes discoloration and death of cotton hypocotyls, while straight-chain heptane shows no phytotoxicity (Morrod, 1976). It has also been shown that β -pinene alters the relative proportions of lipids and causes disappearance of microsomes in Norway spruce needles (Frosch et al., 1989; Klingler and Wagner, 1989).

Translocation

Root ion uptake is inhibited by many organics. For example, nitrophenols, 2,4-D, simazine, and propanil inhibit phosphate uptake, DNP inhibits Ca^{2+} uptake, the organophosphorus insecticide Systox inhibits Cl^- uptake, and phenolic acids inhibit phosphate and K^+ uptake (Barber and Koontz, 1963; Glass, 1973, 1974; Oertli and Ahmadi, 1975; Kaufman, 1976; Morrod, 1976). As uptake of these ions is energy-requiring, the mechanism of reduced uptake may be inhibition of respiration or uncoupling of oxidative phosphorylation.

Herbicides alter the qualitative and quantitative nature of solute transport in plants. The major effects are physical obstruction of the phloem caused by unorganized cell division, blockage by callose formation, localized xylem/phloem tissue injury or death, stimulation or inhibition of metabolic sinks, and decreased transpiration (Ashton and Bayer, 1976). The only reference found for a non-herbicide organic was Wedding and Riehl (1958), who reported that petroleum oil inhibited phosphate transport from roots to leaves in lemon seedlings.

Metabolism

Herbicides

Herbicides have various modes of action. Many interfere with mitochondrial metabolism. Chloro- and nitro-phenols, benzimidazoles, nitriles, and phenoxy acids are uncouplers of oxidative phosphorylation (i.e., the synthesis of ATP is stopped even though respiration continues) (Beever, 1953; Kaufman, 1976; Kirkwood, 1976; Shea et al., 1983). Substituted phenols vary widely in their uncoupling ability (Gaur and Beever, 1959). Other herbicides, including amides, benzoic acids, carbamates, dinitroanilines, halogenated aliphatics, thiocarbamates, triazines, triazoles, and ureas, reduce oxidative phosphorylation by either inhibiting the transfer of energy to intermediates in the formation of ATP, or inhibiting the flow of electrons along the electron-transport chain (Kirkwood, 1976). Glycolysis is inhibited by halogenated aliphatics and phenoxy acids; the latter also inhibit the pentose-phosphate pathway (Kirkwood, 1976).

Many herbicides negatively affect photosynthesis. Inhibition of electron transport in Photosystems I and II occurs by removal or inactivation of intermediate electron transport carriers, or by the herbicide acting as an electron acceptor in competition with normal acceptors. This inhibition is light-dependent. Uncouplers dissociate electron transport from ATP synthesis (photophosphorylation). Some herbicides are both inhibitors and uncouplers. For a comprehensive review, see Moreland and Hilton (1976).

Herbicide effects on intermediate metabolism are numerous. Many inhibit rates of synthesis or degradation of carbohydrates, lipids, proteins, and nucleic acids, or alter the types of these compounds formed (Cherry, 1976; Kirkwood, 1976; Morrod, 1976). However, 2,4-D and 2,4,5-T stimulate lipid synthesis (Morrod, 1976). Some herbicides inhibit nitrite reduction, causing nitrite to accumulate in plant tissues (Klepper, 1979).

Other Organics

Fungicides (e.g., captan) inhibit respiration and photosynthesis at the cellular level in a similar manner to herbicides (Budimir et al., 1976). Evidence exists for inhibition of glycolysis, aerobic

respiration, and uncoupling of oxidative phosphorylation by hydrocarbon oils (Baker, 1970). Ravanel et al. (1989) reported the uncoupling ability of chlorophenol in maple cell suspensions.

Plant Resistance

Plant species differ in their resistance to herbicide effects, and species sensitivity rankings differ among herbicides. Other factors influencing sensitivity are genotype, growth stage, nutritional status, physical damage, cuticular permeability, temperature, water stress, light intensity, leaf area, leaf morphology, transpiration rate, and rooting depth (Aberg and Stecko, 1976; Muzik, 1976). It is well established that the primary causes of "herbicide selectivity" (the pesticide science term for plant sensitivity) are due primarily to three factors: (1) different rates of uptake by the roots and/or shoots; (2) different rates of translocation and differences in the organs and tissues to which translocation occurs; and (3) different capabilities for, or rates of, metabolic detoxification (Sargent, 1976; Wain and Smith, 1976). At the site(s) of herbicide action, species differences in sensitivity often disappear. For example, the Hill reaction in isolated chloroplasts from different plant species is inhibited to the same degree by the same concentrations of simazine and several other herbicides (van Oorschot, 1976). Differential resistance of plant species to hydrocarbon oils has also been observed (Baker, 1970). In the case of the *Umbelliferae*, cell membranes have inherent high resistance to penetration by oils (van Overbeek and Blondeau, 1954).

It is worth noting that plants contain a bewildering variety of organic compounds that are toxic to animals. Most of these are believed to be evolved, qualitative or quantitative, defenses against herbivory. Interestingly, many of these are known phytotoxins, including organic acids and phenols (Duke, 1977). This fact clearly indicates that many plants already possess mechanisms to detoxify some priority air pollutants.

POTENTIAL EFFECTS ON PLANTS

Ecological Effects

When photosynthesis and respiration are inhibited, or ATP synthesis uncoupled from metabolism, the whole-plant reaction should be reduced growth and reproduction. Energy allocated to alleviating the stress of chronic toxin uptake may also reduce the plants ability to produce defensive chemicals. Inhibition of root water or ion uptake may increase allocation to roots at the expense of shoots. Together, these processes lead to lesser competitive ability of affected species. Except near point sources of toxic organics, these effects may occur gradually as small but

continuous atmospheric inputs accumulate. Ultimately, shifts in species composition and dominance may become apparent at the plant community level.

Just which species may suffer most is largely a matter of speculation. For those organics that readily cross the root endodermis, rates of translocation, and hence of bioaccumulation, may be higher for plants with greater transpiration rates (i.e., inherently smaller stomatal resistances). These tend to be early successional species with fast growth rates and among late-successional species that are shade intolerant. Conifers have the highest stomatal resistances of any major plant life form (Komer et al., 1979), yet they also have exceptionally thick, waxy cuticles into which organics may be absorbed. The major route of entry, foliage vs. roots, of organics could play a pivotal role in determining the relative resistances of different plant taxa.

Interactions with other Pollutants

Many organics are weak acids, and their lipophilicity is greater in the unionized form. Penetration of weak-acid herbicides through cuticles increases as solution pH decreases (Fogg, 1948; Sargent and Blackman, 1962; Bukovac, 1976). This phenomenon probably accounts for the enhanced phytotoxicity of nitrophenols and organic acids at low pH (Simon and Beevers, 1951; Simon et al., 1952). As a result, there is a strong possibility that acidified wet deposition increases the phytotoxicity of organics by enhancing uptake (Mullen, 1986).

Biogenic monoterpenes present an interesting case. Like anthropogenic VOCs, they contribute to the photochemical formation of ozone and PAN (Lurmann et al., 1983; Trainer et al., 1987; Chameides et al., 1988) that have been shown unequivocally to reduce photosynthesis and growth of crop and tree species (Reich, 1987). Wagner et al. (1989) have hypothesized that ozone penetrates the mesophyll of conifers, increasing membrane permeability and liberating monoterpenes stored in secretory vesicles. In the presence of ozone, monoterpenes promote the oxidation of sulfur dioxide to sulfate, possibly causing local enhancement of acid deposition to forests (Stangl et al., 1988).

Interactions between different types of gaseous pollutants are well documented (Omrod, 1982). Because terrestrial plant communities are receiving chronic inputs of possibly hundreds of different organic compounds, it is possible that the overall effects in combination are additive, more than additive, or less than additive.

CONCLUSIONS

Thousands of organic compounds are released into the atmosphere each year by human activities, including pesticides, aliphatic and aromatic hydrocarbons (both halogenated and unhalogenated), polychlorinated biphenyls, and phthalate esters. These are transported long distances and reach natural vegetation via wet and dry deposition. Deposition fluxes and velocities have been characterized for only a few organics in a few geographic areas.

The potential for plant uptake and bioconcentration of organics is high and correlated with octanol-water partition coefficients. Greater transpiration rates produce greater root uptake. Foliar uptake of vapor-phase organics has received little attention. Translocation patterns differ among organic compounds. Metabolic detoxification plays a major role in plant resistance, but has been well characterized only for pesticides.

With few exceptions, the modes of action of organics in plants are well-known only for herbicides. A variety of effects by herbicides, usually but not always inhibitory, have been observed on plant growth and morphology; photosynthesis, respiration, and transpiration; cell membranes and ultrastructure; translocation; and respiratory, photosynthetic, and intermediate metabolism. Many of these same effects have been observed with nonherbicide organics. I found no studies on population-, community-, or ecosystem-level effects of airborne organics.

Relevance of Previous Work

As the analysis of the PHYTOTOX database indicated, there is only one class of organics - herbicides - for which the physiological effects on plants are relatively well known. This is hardly surprising, because their purpose is to kill plants, especially weeds. Although it would be desirable to know more about nonherbicide organics, existing knowledge of herbicide effects is helpful in predicting the impacts of organics in general on terrestrial vegetation. For example, herbicides are at times applied aerially to crops or forests, with consequent downwind drift onto adjacent natural plant communities. Some herbicide precursors (e.g., 2,4-dichlorophenol, used to make 2,4-D, and maleic anhydride, used to synthesize pyridazines) are on the EPA's Toxic Release Inventory (U.S. EPA, 1989). Point releases of these, and of the finished herbicides themselves, from sites of manufacture may affect natural vegetation. A few herbicides have other human sources besides pesticide manufacture and use. For example, DNP, DNOC, and other nitrophenols are produced as by-products of smog-forming reactions. Finally, the observed correlations between plant bioconcentration or modes of action and the physicochemical properties of herbicides permit general predictions to be made concerning the phytotoxic effects of nonherbicide organics.

Nevertheless, the literature emphasis on herbicides poses many obstacles to understanding potential phytotoxicity of airborne organics. One obstacle is that the conditions under which herbicides are applied to plants - high concentrations over short time periods - are quite different from those encountered by natural vegetation - low concentrations in a repeated or continuous manner. Significant differences between acute and chronic exposures to the major airborne pollutants have been demonstrated (Lefohn and Runeckles, 1987). Thus, extrapolation from acute agricultural doses to chronic natural vegetation doses may be unwarranted. Another difficulty is the extremely high concentrations of organics used in most dose-response experiments. For example, solution concentrations of 10^3 to 10^9 ng/L are frequently encountered in phytotoxicity studies. Compare these with the concentrations in Table 1.

The best use that we may be able to make of the existing literature is to rank the likelihood of plant uptake of organics according to the vapor pressures, K_{ow} values, and half-lives in soil of the organics (Ryan et al., 1988; Travis and Hattemer-Frey, 1988).

RECOMMENDATIONS

The most critical areas in need of further knowledge are: (1) spatial and temporal patterns of atmospheric concentrations and wet/dry deposition rates; (2) rates of uptake by roots from soil, and of vapors and wet deposition by shoots; (3) translocation patterns; (4) physiological effects from the whole-plant to the subcellular level; and (5) modes of action. In addition, much more emphasis needs to be placed on nonpesticide organics and on native, nonagricultural species growing in natural environments. In all such work, we must use acute or chronic doses that bridge the range of exposures actually occurring in natural ecosystems.

Some specific suggestions are as follows.

- (1) Upgrade routine air, aerosol, and precipitation monitoring networks (e.g., National Atmospheric Deposition Program, National Dry Deposition Network) to measure concentrations of at least the most common and highly concentrated organics.
- (2) Characterize dry deposition to various plant communities. Traditional direct measurement techniques - flux-gradient and eddy correlation (Hicks, 1986) - are difficult due to the very low concentrations of most organics. However, new advances in laser technology - FTIR, lidar, tunable diode lasers - hold promise for use of the flux-gradient technique in the near future.

- (3) Develop methods to measure short-term uptake of organics by plant shoots. These would complement ^{14}C work by distinguishing between cuticular and stomatal absorption, and would permit scaling-up of leaf-level uptake to entire canopies in inferential methods of estimating dry deposition (Hicks, 1986). The technological challenge of generating and measuring low but stable concentrations is great, but the potential gain in predictive capability should be worth the effort.
- (4) Conduct experiments on dose-response relationships of whole plants growing in native soils, including growth, allocation, morphology, water relations, carbon assimilation, and nutrition. Growth chamber, continuously stirred tank reactor (CSTR), and open-top chamber studies, in order, would provide increasing realism in terms of environmental conditions.
- (5) Determine the cellular/subcellular modes of action of various classes of organics. Previous work with herbicides suggests that virtually every translocation and metabolic process is worthy of investigation.
- (6) Measure dose-response relationships for species representative of other major life forms of terrestrial plants besides crops: annual and biennial weeds, perennial herbs, ferns, evergreen and deciduous shrubs, evergreen and deciduous hardwoods, and conifers.
- (7) Develop sensitivity rankings based on absorbed rather than external dose. This approach has yielded better predictive capability for major gaseous air pollutants (Reich, 1987). Because organics vary so widely in their lipophilicity, even within similar structural classes, relationships between external dose and response for one organic are unlikely to apply to other organics.

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