Effects of Pollutants at the Ecosystem Level
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CHAPTER 6
Functional Changes in the Ecosystem

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The ecosystem is the fundamental unit of ecology. Yet the identification and use of appropriate indices to assess the effects of perturbations on 'whole' system functioning have been slow to develop. The focus of ecological research has been on the component populations rather than on the system. This fact is particularly evident in the assessment of toxic pollutants where a preponderance of effort has been spent to identify individual and population effects which can seldom be extrapolated to describe changes at the ecosystem level (Hammons, 1980; NAS, 1981).

The ecosystem is an integrated system with fundamental characteristics which transcend the simple summation of component processes (e.g. Schindler *et al.*, 1980b; O'Neill and Reichle, 1980). Therefore, analysis of the ecosystem as a unit in ecotoxicology is based upon the premise that the system as a whole possesses characteristics which not only reflect the integrated response of component populations to perturbation but, in addition, provide a more comprehensive picture of ecosystem 'status'. The ecosystem is a viable unit and tends to persist through adverse environmental fluctuations, often reflecting changes in structure and efficiency of function, whereas certain individual populations within the

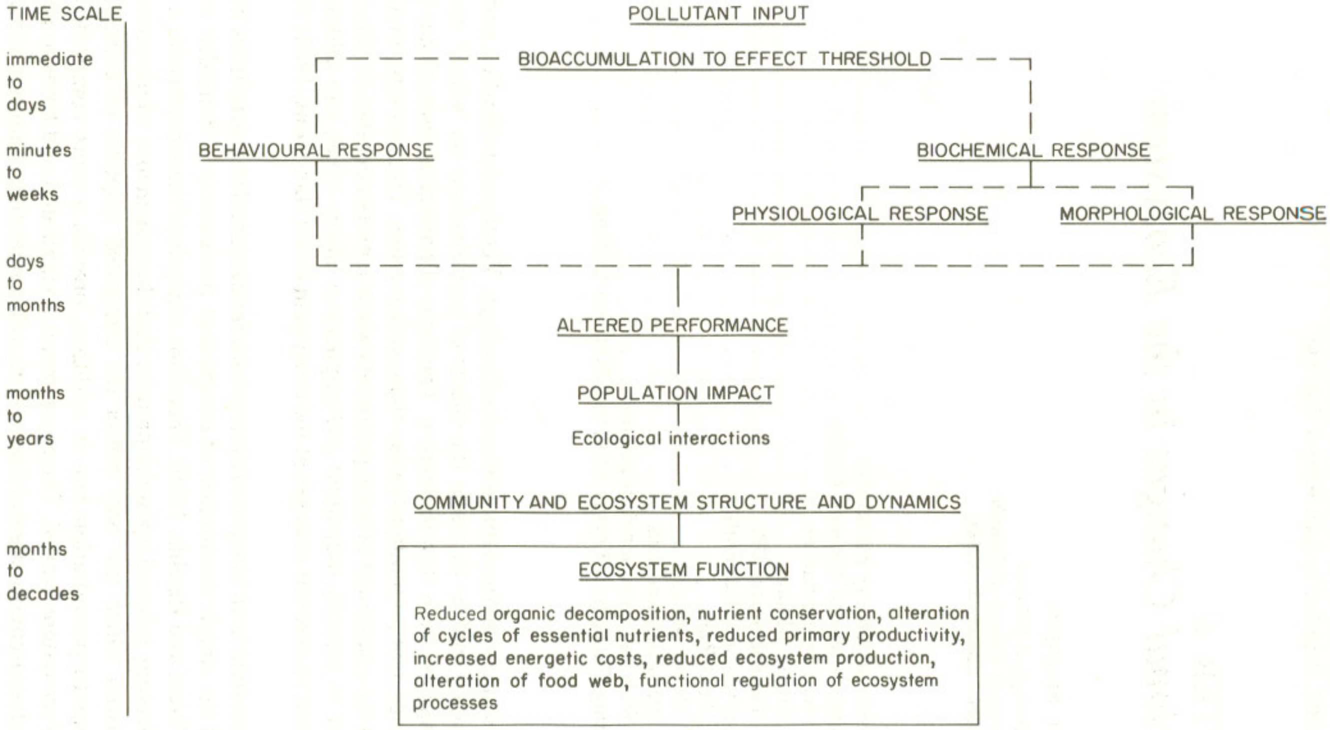

Figure 6.1 A conceptual chronology of induced effects following exposure to toxic pollutants, emphasizing changes in ecosystem function

disturbed community do not survive. Although pollutant-caused perturbations have the potential to influence all components of the ecosystem, the impacts on a single species may have negligible effects on system function. Complex internal feedbacks and controls can minimize overall impact if some form of redundancy exists (see O'Neill and Waide, 1982). For example, sensitive species may be replaced by competitors without affecting the system, or regulation of trophic functions may be maintained by predator flexibility in prey choice. O'Neill and Giddings (1979) have arugued that under conditions of nutrient limitation, major shifts in phytoplankton populations can occur, including the loss of sensitive species but without detectable changes in primary production. On the other hand, critical ecosystem processes such as litter decomposition are sensitive to pollutant stress and display measurable changes without obvious impacts on the highly visible populations normally monitored (Van Voris *et al.*, 1980).

Although there has been a tendencey to emphasize structural characteristics (see Chapter 5) in ecosystem pollution studies, the assessment of effects on the fundamental functional characteristics of biomass production, trophic regulation and nutrient cycling must be encouraged (Barrett *et al.*, 1976; Matthews *et al.*, 1982). Figure 6.1 lists several critical ecosystem processes which can be assessed in response to long-term pollution stress. Changes in primary productivity, energy flow, decomposition, material cycling, and internal regulatory processes provide insight into the dynamics of stress response at the ecosystem level rather than providing a measure of eventual outcome. It is the investigation of these processes which promises the greatest hope for the development of dynamic simulation models which can predict ecosystem level response to loading of toxic pollutants.

6.1 MATERIAL AND ENERGY MOVEMENT

In the early stages, ecosystem analysis did not encourage many investigators to employ a process-oriented approach to pollution studies (see Levins, 1975). A dichotomy of approaches to energy and material analysis were followed (Rigler, 1975). Energy studies were primarily based on trophic models. Mineral cycling investigations explored element availability in environmental pools not generally representative of either trophic levels or populations. However, advances in theory and analysis have encouraged a more holistic framework for assessing ecosystem nutrient and energy processing. Odum (1969) discussed the strategies of ecosystem development in relation to bioenergetic processes, nutrient cycling and regulation of internal homeostasis. Reichle (1975) indicated that one analytical approach is to characterize the nutrient, energy and water budgets of the ecosystem and explain their dynamic behaviour through an understanding of the basic mechanisms governing the internal processes of the system. Specific hypotheses have been proposed that integrate ecosystem energy and material metabolism (Cummins, 1974; O'Neill *et al.*, 1975; Reichle *et al.*, 1975; O'Neill and Reichle, 1980) and a number of authors have proposed the use of functional charateristics in stress assessment (Barrett *et al.*, 1976; Odum, 1977; O'Neill *et al.*, 1977; O'Neill and Reichle, 1980; O'Neill and Waide, 1982).

Ecosystems are essentially energy processing units. The assemblage of organisms and their associated environment interact collectively through the exchange and incorporation of energy and materials. Although there does not appear to be one generally accepted theory of energy maximization in terms of ecosystem persistence, it has been hypothesized that the ecosystem processes energy in a fashion that promotes maximum persistent biomass within the physical and chemical constraints of the environment (Reichle *et al.*, 1975; O'Neill *et al.*, 1975). This hypothesis may be particularly applicable to terrestrial forest ecosystems which generally support a large biomass. Whittaker and Woodwell (1971) indicated that it is biomass accumulation in relation to productivity that reaches a maximum in the climax community of most terrestrial forests.

Application of the above hypothesis to phytoplankton communities in aquatic ecosystems is less certain. In general the biomass accumulation ratio (total organic biomass over net annual productivity) for aquatic systems is less than one, while it is greater than one in terrestrial systems, reaching 2–5 to 30–50 for perennial herbs and mature forests, respectively (Whittaker and Woodwell, 1971). Most aquatic ecologists would certainly support an alternative hypothesis that points to maximization of productivity rather than biomass in plankton-dominated systems (see Hutchinson, 1973). However, under the limitations imparted to the biomass hypothesis by the phrase 'within the physical and chemical constraints of the environment', it would appear to be generally applicable as a basis for analysis of any ecosystem.

The ecosystem can minimize and counteract the influence of environmental stress through population shifts and interactions. According to the hypothesis, unless a population contributes to the maintenance of persistent maximum biomass either through efficient photosynthetic energy conversion at the autotrophic level or through the efficient upgrading of energy quality, regulation of internal homeostasis, and/or cycling of essential nutrient at the heterotrophic level, there is strong negative selection against that population. Therefore, the ecosystem as a unit of investigation, is characterized as persisting in spite of perturbation, through dynamic shifts in its nutrient and energy metabolism. Populations are 'sacrificed' to preserve the integrity of the ecosystem, much as cells grow and die even as the organism persists. Of course, we cannot assume the same level of integration in an ecosystem as exists in the centralized organization of an organism.

As functional processes within the ecosystem, energy and material movements are intimately related. Within the constraints of the physical environment, the rate of the primary energy transformation process, photosynthesis, is regulated by essential element availability. There is an array of elements required for growth, reproduction, replacement of structural parts and general maintenance of all plants and animals. Mineral nutrients and food are often exchanged in the same community between producer and consumer levels, although the relative rates of usage are not generally equivalent. Therefore, a fraction of the energy processed by the ecosystem is expended in nutrient recycling and biomass retention (O'Neill and Reichle, 1980).

The cycling of carbon is most closely linked to energy flow since primary production is usually measured as organic carbon accumulation and respiration cost as carbon dioxide release. Other macronutrients and certain essential trace elements are selectively retained by the biota, thus these elements may pass through the food chain more slowly than bound chemical energy. Species retain elements and energy in their biomass. Maximum development of biomass storage is best characterized by the vast structural pool in forested systems. These huge biotic structures represent a living reservoir of energy and materials to the ecosystem; however, this reservoir is maintained only at a significant energy cost. Systems also have a large alternative material and energy base consisting of detrital organic material.

However, it is not merely the retention of elements which insures ecosystem persistence. Both a means to regulate remobilization of these nutrient resources (a major function of the consumer communities, in particular, decomposers) and a mechanism to regulate functions within the consumer community are essential. Consumer interactions thus contribute to the overall homeostasis of the ecosystem. Efficient remobilization of nutrients requires energy expenditure, however, and there are costs in regulation and homeostasis.

In all but plankton dominated ecosystems, the bulk of the net primary productivity enters the decomposition subsystem directly as dead organic matter (detritus). The faeces and carcasses of the consumer community also contribute to the detrital input to decomposition. The decomposition system is immensely important to both energy metabolism and efficient nutrient mobilization and conservation. Decomposers which utilize the organic energy of detritus also function to maintain essential nutrient elements in forms available for plant uptake.

Consumer species function as regulators of the major processes of primary productivity and decomposition, either through feeding interaction, competition, alteration of the environment or through performance of some unique functional role such as pollination. Within the ecosystem, such regulation is achieved through the diversity of the controlling species, the complexity of interactions or the unique and specific character of the feedback. Host–parasite and symbiotic interactions exemplify the latter control mechanism. The importance of any one mechanism of consumer control would depend on the system itself and on the species' evolution of adaptations to cope with fluctuations in the environment (Ricklefs, 1973). Species interactions which contribute to ecosystem regulation often have characteristic response time lags which increase the instability of the interaction. Therefore, natural and man-related perturbations to the system may not be recognized until some time after their introduction, as noted by the time scale of responses in Figure 6.1.

The interrelationship of energy and material movements can be depicted simply, as in Figure 6.2. Although this representation was developed for a terrestrial ecosystem, it is generally applicable to aquatic systems, given that there has been no demonstration of an equivalent process for withdrawal of nutrients from senescent leaves, and there is little or no dissolved pool of refractory organic compounds which can be classified as humic. There are also some

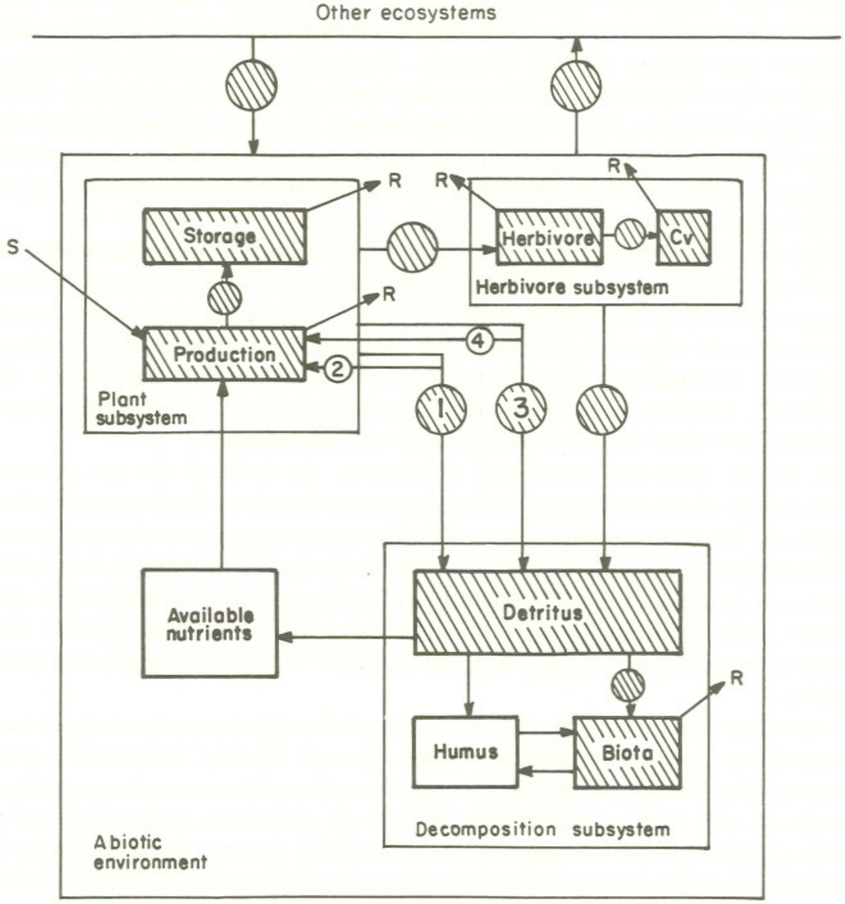

Figure 6.2 Nutrient and energy pools and fluxes within ecosystems. Pools and fluxes of both energy and nutrients are shaded. 1: litter production; 2: withdrawal from senescent leaves; 3: leaching losses; 4: reuse of dissolved organic carbon (DOC) by algae; S: solar radiation; R: respiration losses. The uptake and release of gases by all three subsystems are implicit

obvious differences in energy and material processing in terrestrial and aquatic ecosystems. Terrestrial systems are based on structurally complex vascular plants where the 'detritus' food chains are quantitatively more prominent. Biomass storage and efficient nutrient recycling are highly developed. Lakes and marine ecosystems are based on rapidly reproducing autotrophic populations supporting well-developed 'grazing' food chains (Wiegart and Owens, 1971). Most aquatic systems, particularly streams, can be conceptualized as being greatly dependent on the surrounding watershed for nutrient input (Likens and Bormann, 1975) although there is some evidence of the importance of internal nutrient recycling in freshwater lakes. Axler *et al.* (1981) reported that during most of the growing season, nitrogen regeneration via zooplankton excretion and microbial mineralization was critical to phytoplankton growth in Castle Lake, since levels of dissolved inorganic nitrogen were insufficient to support the rates of primary production measured. These differences emphasize the importance of examining nutrient conservation processes in terrestrial systems under pollution stress, while considering changes in primary production and consumer regulating processes in perturbed phytoplankton-based aquatic systems. This would not ignore the importance of recycling of essential elements in lake and marine systems, but would place emphasis on those specific processes governing essential element availablity such as nitrogen fixation, nitrification, ammonification, consumer regeneration of ammonia and sediment–water interchanges. Nor would such an approach ignore direct pollutant interference with terrestrial productivity or yield when such effects are measureable.

This survey builds a case for examining toxic pollutant interference with ecosystem function. (It would appear that the theory and methodology would be quite applicable to physical perturbations as well.) The focus will be on productivity and decomposition subsystem processes, and the ways in which these processes are regulated.

6.2 DECOMPOSITION AND ELEMENT CYCLES

Toxic pollutants can interfere with the decomposition process itself and interrupt internal recycling of essential elements, particularly nitrogen. The decomposition process forms the major link between nutrient availability and primary production through its control of the breakdown of organic matter, essential element immobilization and release, and soil humus formation. Decomposition is also the process through which a major portion of all heterotrophic energy is expended (Heal and MacLean, 1975). In unperturbed systems where quantities of 'available' inorganic forms of nutrients are seldom in excess of plant demand, essential element cycles, such as that for nitrogen, are particularly vulnerable to pollution disruption. Aside from their role as mineralizers, microorganisms contribute substantially to nutrient conservation through nitrogen fixation and essential element immobilization in their cells.

Decomposition processes in terrestrial ecosystems have been extensively reviewed (Witkamp and Ausmus, 1976; Lohm and Persson, 1977; Swift *et al.*, 1979). A number of reports have detailed the decomposition process in aquatic systems, emphasizing its importance in energy movement rather than nutrient cycling (Fisher and Likens, 1973; Cummins, 1974; Boling *et al.*, 1975; Saunders, 1976). Woodall and Wallace (1975) indicated that streams function primarily through the use and transport of nutrients from the watershed. However, Likens (1975) suggested that within stream boundaries, nutrients may be cycled very rapidly among living components, nonliving components or both. Filter feeders may play a significant role in such recycling processes (Wallace *et al.*, 1977). The study of critical regeneration of nitrogen in Castle Lake, previously cited (Axler *et al.*, 1981), is an example of current research to determine the importance of element recycling by biota in lake ecosystems, in relation to primary productivity.

Decomposition can be divided into three processes: (1) leaching, (2) faunal breakdown, (3) microbial mineralization. Leaching processes affect element movement from live plant tissue and detrital materials. The process is primarily physical in nature (Witkamp and Frank, 1970) although the rate of leaching can be influenced by the extent of fragmentation and breakdown of leaf litter by invertebrate and microbial feeders. Extracellular release by phytoplankton in aquatic systems provides a biological mechanism for the transfer of organics to the dissolved pool. The largest portion of dissolved organics are leached early in the decomposition process. A diverse community of decomposer organisms effects element cycling by means of mechanical comminution of detritus, enzymatic breakdown of ingested matter, channelization of woody substrates and colonization of detritus by microbes (Witkamp and Ausmus, 1976). Microbial decomposition, which generally begins before leaf senescence, leads to the release of inorganic elements. Microbial cells immobilize considerable amounts of N, P and K, retaining them against leaching loss (Ausmus *et al.*, 1976).

The rate of decomposition is regulated by three controlling factors: (1) the physico-chemical environment, (2) the available resource (detritus) quantity, (3) the resource quality. Pollution input generally affects decomposer activity through direct toxic stress (i.e. changes in the chemical environment), although toxic organic pollutants (oil, industrial organic effluents, pesticides) can play an additional role by affecting the other controlling variables.

There have been few ecosystem studies directed specifically at determining the effects of toxic pollutants on the decomposition process and the efficiency with which essential elements are conserved and cycled. However, there presently appears to be a theoretical base and a developed experimental technique to support such studies (Witkamp and Ausmus, 1976). It is important to consider the fact that in terrestrial systems, during the early successional stages, nutrient recyling is only minimally developed and the systems are 'leaky'. Reversion of normally element-conservative, mature systems to a state in which they export excessive levels of calcium, magnesium and inorganic nitrogen, is convincing evidence of the breakdown of their characteristic internal regulatory mechanisms. This type of retrogression infers a reduction in the biotic control of nutrients. The investigations at the Hubbard Brook Forest watershed have provided much experimental impetus for the study of nutrient dynamics and their control processes as a means of determining the effects of perturbations on ecosystem function (Likens *et al.*, 1970; Gosz *et al.*, 1973; Likens and Bormann, 1975). O'Neill *et al.* (1977), using a series of terrestrial microcosm experiments involving additions of either 100 mg cm^{-2} Na_2HAsO_4 or 11 mg cm^{-2} Pb, demonstrated that pollutant disruption of the nutrient cycle, as measured by the net rate of leached soil nutrients (Ca and NO_3—N), provided a more sensitive and reliable measure of system disturbance than did population numbers, biomass or microbial diversity.

Several recent studies of specific ecosystem pollutant problems such as acid precipitation (Abrahamsen, 1980; Bjor and Teigen, 1980; Norton *et al.*, 1980; Wright and Johannessen, 1980; NRCC, 1981a) and heavy metals (Jackson and Watson, 1977; Jackson *et al.*, 1978; Hughes *et al.*, 1980b; Lepp, 1981) have provided additional evidence of decomposition and nutrient cycling disruptions, further illustrating the implications of long-term disturbances on the metabolic functioning of a system. Although a preponderance of the information on the disruption of decomposition processes and their function in material conservation and recycling is from laboratory or microcosm and short-term small-scale field investigations, it seems clear that such processes should be examined when evaluating ecosystem perturbations.

6.2.1 Acid Precipitation

Acid precipitation is a very topical issue and a damaging pollution problem. There is considerable evidence that directly through toxic effects and indirectly through lowering of environmental pH, atmospherically borne H_2SO_4 and HNO_3 have caused extensive disruption of material conservation and cycling in both terrestrial and aquatic systems.

Through-fall studies have indicated increased foliar leaching with increased incidence of acidic rain (Abrahamsen *et al.*, 1976; Cronan, 1980; Cronan *et al.*, 1980). Abrahamsen *et al.* (1976) showed that concentrations of metal cations increased with the fall of acid rain. Previously, cation exchange for hydrogen ion in the tree crown had been postulated to explain foliar leaching (Eaton *et al.*, 1973), although processes such as foliar exudation are likely of importance (Cronan, 1980). Potassium (K^+) efflux from lichens has been correlated with SO_2 levels and the acidity of precipitation (Nieboer *et al.*, 1976; Tomassini *et al.*, 1977). Acidification experiments in Norway demonstrated that rain pH significantly influenced the amount of calcium, magnesium and potassium in through-fall (Figure 6.3). It is probable that a large portion of the through-fall enrichment

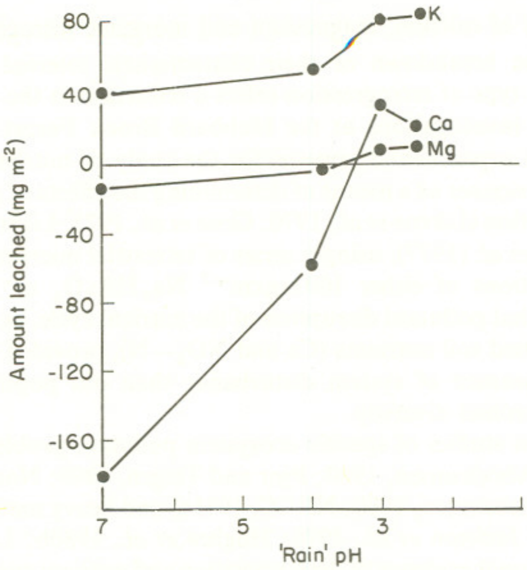

Figure 6.3 Effect of pH of simulated rain on leaching of Ca, Mg and K from spruce crowns. Average of two treatments of 50 mm 'rain'. Before passing the tree crowns the 'rain' contained 315, 35 and 35 mg m^{-2} of Ca, Mg and K, respectively. (Reproduced by permission from Abrahamsen *et al.*, 1976)

in Cl^-, SO_4^{2-}, Na^+ and H^+ is derived from dry deposition rather than from leaching (Abrahamsen *et al.*, 1977). Wood and Bormann (1975) demonstrated increased foliar leaching of nutrient cations (Ca^{2+}, Mg^{2+}, K^+) to be a function of increases in the acidity of an artificial mist applied to greenhouse plants. Increased leaching was demonstrated with no visible foliar damage at pH 3.3 but cation levels in the leachate were considerably elevated with tissue damage below pH 3.0. Leaf cuticle erosion, accelerated by acids (Shriner, 1976), and cuticular abrasion by other environmental stresses (Tukey and Morgan, 1963), may account in part for accelerated foliar leakage in acid rain disturbed systems. Mathematical techniques to separate crown leaching components were recently described by Lakhani and Miller (1980).

There is also evidence suggestive of accelerated nutrient loss due to structural damage and root leakage accompanying decreases in plant resistance to pest infestation under SO_2 stress (Knabe, 1976). Pest invasion can eventually kill trees, reducing their long-term effectiveness as nutrient-conserving units. Polish forest soils exposed to average annual SO_2 concentrations greater than

0.8 mg m^{-3} are becoming acidic, favouring establishment of root-destroying fungi such as *Armillaria mellea*, bringing about short-term increases in root leakage which eventually lead to disruption of the ability of plants to take up nutrients (Grzywacz and Wazny, 1973).

Perhaps more detrimental to plant productivity is the increased acidic leaching of mineral and detrital elements from soils (Rorison, 1980), which results also in the release of potentially toxic heavy metals into ground and surface waters (Beamish and Van Loon, 1977; Cronan *et al.*, 1978; Hutchinson, 1980). This loss is particularly damaging in the nutrient deficient soils of many forested ecosystems (Engstrom, 1971). Overrein (1972) observed dramatic releases of calcium from the root zone in forest soils exposed to precipitation with a pH of 3.0. Lysimeter studies have demonstrated that simulated acid rain (pH 2.5) induced net losses of K, Ca, Na, Mg, Mn, Al and NO_3 and NH_4 from podzol-type soils (Bjor and Teigen, 1980). It was the leaching of calcium and magnesium which was most affected by acid rain with a pH in the range of 3–4, and this effect was most noticeable in the surface layer of the soil profile. Figure 6.4 illustrates the effects of acidification on levels of calcium, magnesium and potassium in soil, leachate and vegetation. The leaching of nitrogen is generally

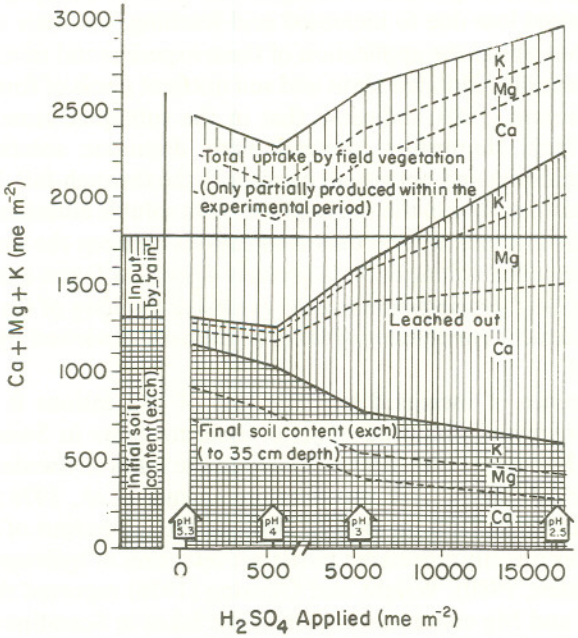

Figure 6.4 Acid rain treatment effects on calcium, magnesium and potassium in soil, leachate and vegetation. (Reproduced by permission from Bjor and Teigen, 1980)

much less than the input by precipitation (Abrahamsen, 1980; Cronan, 1980) and, therefore, the net losses of Ca, Mg and Mn from the soil nutrient pool are of greater concern. The crucial question is whether or not the increases in weathering of minerals due to acidification can compensate for the increased leaching losses in surface and ground-water runoff.

The degree of leaching increases considerably as a function of decreases in pH of the precipitation (Abrahamsen *et al.*, 1977; Abrahamsen, 1980). However, the quantity of leached cations that were measured were not found to be equivalent to the amount of acid added (H^+). These results lend support to the theories advanced by Wiklander (1975, 1980) who called attention to the low efficiency of hydrogen ions in exchanging metal cations in acid soils. Application of 50 mm of 'rain' ($pH < 3$) to soils significantly reduced their base saturation and lowered soil pH (Abrahamsen *et al.*, 1976). Aluminium, because it is common in soil minerals and is chemically active, plays a dominant role in regulating soil solution acidity. High levels of Al may be brought into soil solution to buffer soils receiving acid rain (Voigt, 1980; Johnson *et al.*, 1981). Abrahamsen and Stuanes (1980) reported that simulated acid rain produced effluent solutions differing in pH, SO_4^{2-} and Al concentrations from soils of the same type as one another but dominated by different plants. Leaching studies have consistently demonstrated potential nutrient loss due to increased acid leaching, but their small scale has raised questions about the application of these experimental results to the more extensive, internally regulated plant and soil nutrient pools of forests. However, data from Cronan (1980) indicated that in the subalpine zone of the White Mountains, New Hampshire, mineral acids dominate solution chemistry. Calcium, magnesium and potassium increase in the through-fall. Levels of these cations gradually decline in the soil leachate, with soluble aluminium accounting for most of the increase in total dissolved cations between the through-fall and forest floor percolate solutions. In a severely disrupted forest ecosystem near a metal smelter, acid precipitation caused extensive leaching of Ca from the soil, with the consequent enrichment of lakes in the area (reviewed by Gorham and McFee, 1980).

The occurrence of increased leaching loss of soil cations is supported by evidence of increased dissolved mineral concentrations in Swedish rivers, as discussed by Malmer (1976), and in some remote lakes in Sweden and Canada which receive substantial acid precipitation (Almer *et al.*, 1978; Dillon *et al.*, 1980). In small watersheds on granitic bedrock the net output of combined Ca, Mg and Al was directly correlated to the net retention of hydrogen ion (Wright and Johannessen, 1980). Wright and Gjessing (1976) reported that there were increased Ca and Mg concentrations in acidic lakes in Scandinavia and North America relative to levels in unaffected lakes in the same geographic areas. The net export of calcium, magnesium and potassium as previously described is due, in part, to natural weathering, but a major fraction results from acid-induced leaching from normally element-conservative plant and soil systems. In addition, the base-impoverished surface sediments in acid lakes in the Adirondack Mountains indicates increased leaching within an aquatic system (Galloway *et al.*, 1976).

The sensitivity of certain decomposer organisms to an acid pH environment has been established, but the effect of precipitation-induced acidification on the functional effectiveness of the decomposer community is less well defined. Groups like protozoa and earthworms are very rare in most soils with pH below 4 (Stout and Heal, 1967; Satchell, 1967), however, Wood (1974) found extensive earthworm colonization in the organic and mineral-rich but acidic ($pH \leq 4.5$) alpine soils of Mount Kosciusko, Australia. Although Abrahamsen *et al.* reported in 1976 that they had found no significant effects of acid rain on soil fauna, later studies indicated that populations of *Cognettia sphagnetorum*, which feed primarily on litter and associated microbes, were significantly reduced in experimentally acidified plots with litter-humus pH generally less than 5 (Lundkvist, 1977; Abrahamsen *et al.*, 1980).

In preference experiments, Lumbricid and Enchytraeid worms either selectively colonized basic soils or avoided humus $pH < 3.9$ (Hagvar, 1980). The abundance of the total Enchytraeid group was significantly reduced in acified forest plots where pH had been lowered to 4.1, 4.2 and 4.7, respectively, in the top three soil profiles. The vertical distribution of *Cognettia sphagnetorum* also changed in acidified plots, as the main part of the population was found not in the humus-litter layer, but rather, in a lower profile (Bååth *et al.*, 1980a, b). Other important soil invertebrates such as mites (Acari) and spring tails (Collembola) are affected differently by acid precipitation. The total abundance of all mites appeared to be unaffected by rain acidity, pH 4 to 2.5, in experimentally acidified soil plots (Bååth *et al.*, 1980a, b; Abrahamsen *et al.*, 1980). However, in similar experiments, the total numbers of Acari were decreased in soil with pH 2.5 to 4, as was the vertical distribution of the Oribatid group (Hågvar and Amundsen, 1981). It was suggested that reduced abundance of soil invertebrates was best explained by the correlation between soil pH and reproductive success. On the other hand, the total abundance of Collembola increased in acidified plots, pH 2.5 to 4 (Abrahamsen *et al.*, 1980), suggesting release from competitive or trophic constraints. The lengths of FDA-active fungi and the numbers, biomass and cell size of soil bacteria have been shown to be reduced by experimental acidification of soils to a pH of 4.2, while total fungal mycelium appear to increase in abundance (Bååth *et al.*, 1980a, b; Lohm, 1980). Isolated soil bacteria were unable to grow at pH values less than 4. Acid treatment also caused marked changes in the physiological abilities of soil bacteria. In acetate and in 'nitrogen free' media, growth was impaired (Bååth *et al.*, 1980a).

Aquatic crustaceans such as the detritus-feeding amphipod, *Gammarus lacustris*, are not found in Norwegian lakes below pH 6, nor are oligochaete worms abundant in these lakes' deep sediments (Leivested *et al.*, 1976). Minshall and Minshall (1978) found that the mortality rate for *Gammarus* in water with a pH of 5–6 was twice as high as in pH 6–7 water. In general, the number of species in acid lakes decreases with pH (Almer *et al.*, 1978; Økland and Økland, 1980) although it is assumed that pollutants associated with acidification (e.g. metals, particularly aluminium) may also restrict faunal abundance. Mossberg and Nyberg (1979) reported that the number of species declined at a pH of 4.2 to 5 in Norwegian lakes. Reducing the pH in a stream from 5.4 to 4.0 reduced macroinvertebrate standing crop (Hall *et al.*, 1980). Macroinvertebrates are less active in leaf decomposition in naturally acidic streams (in Hendrey *et al.*, 1976). Although no marked differences in the content of fine particulate organic matter (FPOM) or dissolved organic material (DOM) were detected between an acidic and a non-acidic stream, the breakdown of leaf material was much slower in the former system (Friberg *et al.*, 1980). The biomass of invertebrates per leaf pack was less, the number of species was less and the community of functional feeders contained far more 'shredders' and fewer 'scrapers' in the acidified stream (pH 4.3–5.9) than in the nonacidic one (pH 6.5–7.3). The reduced breakdown of leaf material could be the direct result of organism sensitivity to low pH or an indirect response to a reduced microbial community associated with detritus. Boling *et al.* (1975) found that certain macroinvertebrate detrital feeders in streams prefer 'conditioned' (microbially colonized) leaves, which are of increased nutritional value. Physiological studies of decomposer bacteria indicate that very few kinds function actively below pH 4 (Doetsch and Cook, 1973). Long- and short-term studies of the effects of soil acidification showed that heterotrophic bacterial counts were severely reduced, resulting in decreased microbial respiration (Bryant *et al.*, 1979). The effects of aquatic acidification on microbial activity were determined in laboratory experiments by examining the decomposition of peptones (Bick and Drews, 1973). Total bacterial cell counts and the numbers of ciliated protozoa decreased with decreasing pH. The investigators noted that for the peptone substrate, decomposition and nitrification were also reduced as the pH decreased, and oxidation of ammonia ceased below pH 5. At pH 4 and lower, the numbers of fungi increased, however. In acidified lakes the effect of reduced pH on decomposition processes appears to be greater in the littoral rather than in the profundal sediments (Gahnström *et al.*, 1980). Sphagnum mats accompanied by dense filamentous algae have been observed covering acid lake sediments, restricting element movement from the sediments (Hendrey and Vertucci, 1980).

Laboratory studies have provided further evidence for reduction of decomposer metabolic activity under acidified conditions. In soil tests, a highly significant correlation was found between the relative amount of CO_2 produced and the exchangeable hydrogen ion content of the soil (Francis *et al.*, 1980). Experiments using glucose and glutamic acid substrates demonstrated that reduced pH led to a shift in the dominant organism from bacteria to fungi, with an accompanying decrease in zooflagellate fauna and consequent decrease in the consumption of oxygen (Leivestad *et al.*, 1976). The extent of the inhibition of glucose oxidation and the fall in pH were found to be proportional to the period of exposure to SO_2 (Grant *et al.*, 1979). Oxygen consumption, used as a measure of the rate of decomposition of homogenized leaf litter, was reduced by 50 per cent when the pH decreased from 7.0 to 5.2, and no adaptation to lower pH was achieved over a 3-week period (Traaen, 1974). In both natural and artificial sediment cores, the rate of oxygen uptake indicated that heterotrophic microbial activity was reduced when the pH of overlying water was decreased to below the neutral range (Leivestad *et al.*, 1976).

Although the effects of acid rain on decomposition may not be obvious for some time after exposure (Johnson and Shriner, 1980; Roberts *et al.*, 1980), the end results of decreased number and activity of decomposer organisms are a reduction in the decomposition rate and the accumulation of coarse detrital material in the ecosystem. The decomposition rate of lodgepole pine needles increased significantly above pH 3.5, whereas at a pH of 1, no decomposition took place (Abrahamsen *et al.*, 1977). The rate of decomposition of Scots pine needle and root litter was significantly reduced by application of acid rain for a period greater than one year, which lowered soil pH by 0.5 units to 4.2 and 4.1 in the top horizon (Bååth *et al.*, 1980a; Lohm, 1980). There was also a reduction in nitrogen retention in the needle litter of the acidified plots. Decomposition of cellulose was significantly retarded with increased rain acidity in some experiments (Ruschmeyer and Schmidt, 1958; Baath *et al.*, 1980a); however, this finding has not been consistently duplicated (Hovland and Abrahamsen, 1976). Recently, Killham and Wainright (1981) reported cellulose degradation to be only marginally inhibited by atmospheric pollution from a coke plant which reduced decomposition of deciduous leaf litter by 35 per cent. There are few data which document increased litter accumulation associated with pH decreases. Freedman and Hutchinson (1980b) observed a trend toward higher standing crops of litter at sites closer to a nickel smelter, but heavy metal levels as well as acidity in the litter were significantly higher than normal. Litter-bag experiments in acidic stream waters have indicated reduced decomposition (Hendrey *et al.*, 1976). Similar results have been reported for acidic lakes (Traaen, 1980; Francis *et al.*, in press). Figure 6.5 illustrates decreases in the per cent weight loss of leaf litter with increasing lake acidity and an associated decrease in bacterial colonization. There were species-specific differences in decomposition rate which appear to be associated with microbial colonization and activity. Abnormal accumulations of coarse organic detritus have been observed on the bottoms of six Swedish lakes where pH has decreased by more than 1.5 units in the past 30 to 40 years (Grahn *et al.*, 1974).

In both Sweden and Canada, acidified lakes have been treated with alkaline substances to determine the effect of neutralizing pH on the decomposition processes. Such treatments have complex effects on water chemistry, but have resulted in increases in heterotrophic bacteria, increased microbial activity and an acceleration of organic decomposition processes (Andersson *et al.*, 1975; Scheider *et al.*, 1975).

Acidification of the environment directly and indirectly affects the nitrogen

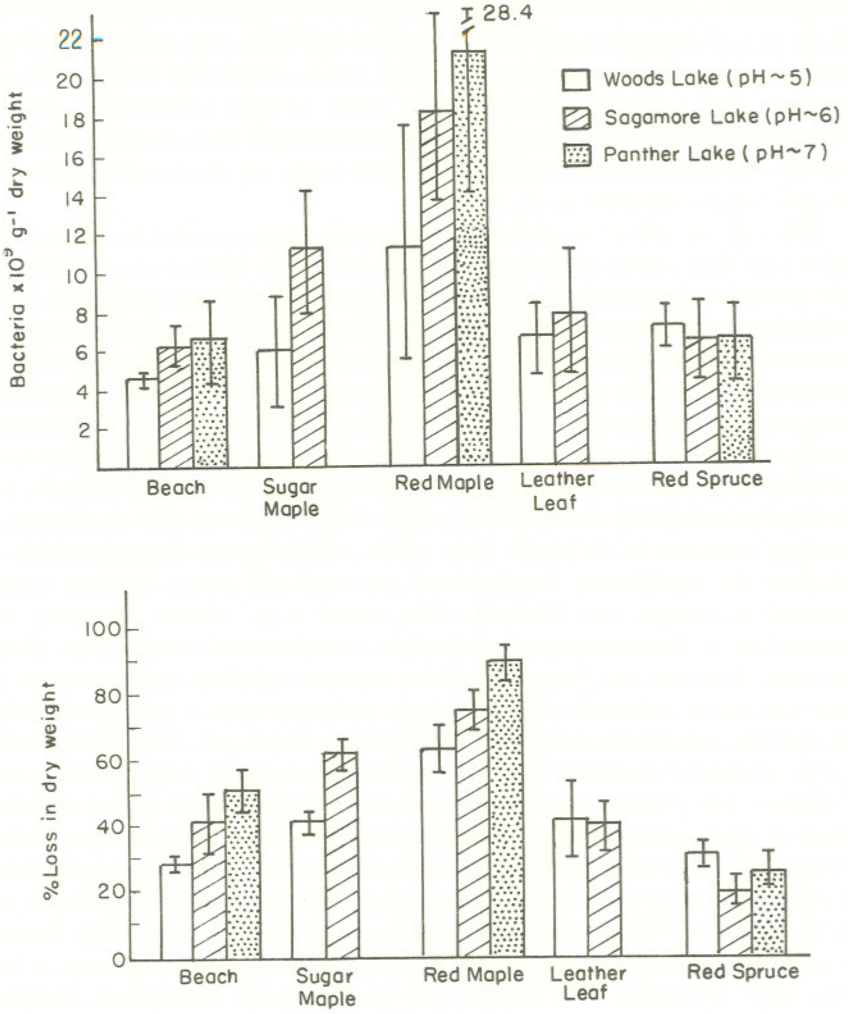

Figure 6.5 pH influence on microbial colonization of leaf litter and on leaf decomposition in three Adirondack lakes. (From Francis *et al.*, in press. Reproduced by permission of Ann Arbor Science Publishers)

cycle. Increases in soil acidity adversely affect the root–mycorrhiza relationship, presumably disrupting the nitrogen fixing activities of associated bacteria. The root nodulation process which is the prelude to nitrogen fixation is particularly sensitive to soil acidification (Alexander, 1980a). In addition, the numbers of infective root-nodule bacteria are often reduced to exceedingly small populations as the pH value falls below 5.0 (Rice *et al.*, 1977). Alexander (1980a, b) concluded that the nitrogen inputs resulting from the legume-*Rhizobium* symbiosis would likely be greatly lowered as soil acidity increases and the same effects would reduce nonsymbiotic fixation. Nitrogen fixation by free-living bacteria in naturally acid and pH-adjusted soils did not take place at or below pH 4.7 and at pH 5.8 the amount of nitrogen fixed was 1000 times less than in soils at pH 6.4 (Francis *et al.*, 1980). Acid water (pH 5) also markedly reduced the rate of fixation in litter samples (Denison *et al.*, 1977). Some nitrogen-fixing lichens such as *Lobaria oregana*, very important to the nitrogen balance of mature Douglas fir forests, are particularly sensitive to acid rain (Tamm, 1976). Wodzinski *et al.* (1977) demonstrated that nitrogen-fixing blue-green algae were one of the microbial groups particularly sensitive to acidification.

Several investigators have reported reductions in nitrification rates in acidified artificial and natural soils (Hovland and Ishac, 1975; Tamm, 1976). Autotrophic nitrifiers were demonstrated to be very sensitive to acidic conditions (Francis *et al.*, 1980). Remacle (1977) reported that nitrification rates decreased with decreasing pH while ammonia production increased until pH fell below 5.1. Tamm *et al.* (1977) observed that acidification of soils decreased carbon dioxide evolution, with accompanying increases in ammonification and decreases in nitrification. They concluded that the decreased microbial activity was more pronounced for nitrogen immobilization processes than for decomposition processes in general. However, it should be noted that the importance of reduced nitrification in acidified systems is not totally understood. Indeed, less nitrogen in the leachable nitrate form may in fact reduce net nitrogen loss. Tamm (1976) found that repeated acid treatments of soils reduces both nitrification and ammonification, indicating a severe disruption in organic nitrogen mineralization processes. Inhibition of denitrification has been reported for bacteria in soil acidified to a pH of 4.1–4.2 (Bååth *et al.*, 1980a). One complication that arises when interpreting changes in the nitrogen cycle is the input of nitrogen compounds from the HNO_3 portion of the acid precipitation. The impact of these compounds as fertilizer sources is not yet fully understood, although Bengtson *et al.* (1980) reported that nitrogen oxides were taken up by Scots pines in amounts linearly related to NO_x concentrations in the field.

Little is known about the effects of acidification on sulphur-cycle bacteria although Schindler *et al.* (1980a) found that sulphate-reducing bacteria neutralize a considerable level of acid input to lakes, and sulphate reduction to sulphide in soils is markedly inhibited below pH values of 6 (Connel and Patrick, 1968). Both the chemistry of phosphorus and its uptake by algae are pH sensitive, and the solubility of heavy metal ions increases at low pH, suggesting that synergistic adverse effects may accompany ecosystem acidification. Very little is known about the consequences of the loss of long-term essential element storage in the biomass of large consumers (fish), eliminated from acidified aquatic systems.

In summary, field and laboratory experiments have indicated that acid precipitation interferes with ecosystem nutrient conservation and cycling processes through several mechanisms:

1. Increasing leaching export of essential cations.
2. Bringing heavy metal ions into solution.
3. Inhibiting organic decomposition and shrinking the available nutrient pool.
4. Inhibiting N_2 fixation and reducing nitrification and ammonification (under severely reduced pH conditions).

6.2.2 Heavy Metals

The reported effects of metal pollution on decomposition and element cycling are quite similar to those previously discussed for acid precipitation. There is no reason to suggest that low pH need accompany metal pollution in explaining the similarity in patterns of disruption; however, metals and SO_2 are at times closely interrelated (see review by Haines, 1981). They can be derived from the same industrial source. Acidity can enhance metal toxicity (Skidmore, 1964) and increase metal solubility (Stumm and Morgan, 1981), bringing toxic concentrations of certain metals (e.g. aluminium) into solution even at pH values not considered harmful (Cronan and Schofield, 1979).

O'Neill *et al.* (1977) reported that lead-contaminated (11 $\mathrm{mg\,cm^{-2}}$) terrestrial microcosms showed no signs of growth sensitivity even after 9 months of exposure. However, the mean calcium level in the soil leachate, 29.4 $\mathrm{mg\,l^{-1}}$, was significantly higher than the mean of 20.3 $\mu\mathrm{g\,l^{-1}}$ measured for unexposed microcosms. Leached nitrate levels were also elevated but were not statistically higher than for control plots. The treated microcosms continued to lose nutrients long after exchange processes would have equilibrated, indicating a disruption of calcium immobilization processes, accelerating Ca export from the system. Jackson *et al.* (1978) found a similar sustained leaching effect for Ca and NO_3—N due to synergistic heavy metal contamination in an intact forest microcosm exposed to Pb, Cd, Zn and Cu at levels of 11.0, 0.128, 0.748 and 0.161 $\mathrm{mg\,cm^{-2}}$, respectively. The soil pool of extractable nutrients showed signs of depletion after 20 months of contamination. Arsenic-induced stress stimulated loss of $PO_4 - P$, $NO_3 - N$, $NH_4 - N$ and DOC from a grassland microcosm (Jackson *et al.*, 1979). The advanced stage of pollution response near a lead smelter is characterized by nutrient depletion in the soil and litter pools (Figure 6.6) (Jackson and Watson, 1977). Depletion of Ca, Mg and K is correlated with distance from the metal source. Severely metal-stressed terrestrial ecosystems can support only sparse vegetation and later show signs of general material erosion, emphasizing the deterioration of nutrient conservation mechanisms (Jordan, 1975).

There is little evidence to suggest that aerial metal pollution stimulates foliar leaching of nutrients as was documented previously for acid precipitation. Severe heavy metal dusting can cause foliar injury to plants (Kraus and Kaiser, 1977), which could eventually contribute to element export. There is some information suggesting that toxic metals stimulate extracellular release of dissolved organic

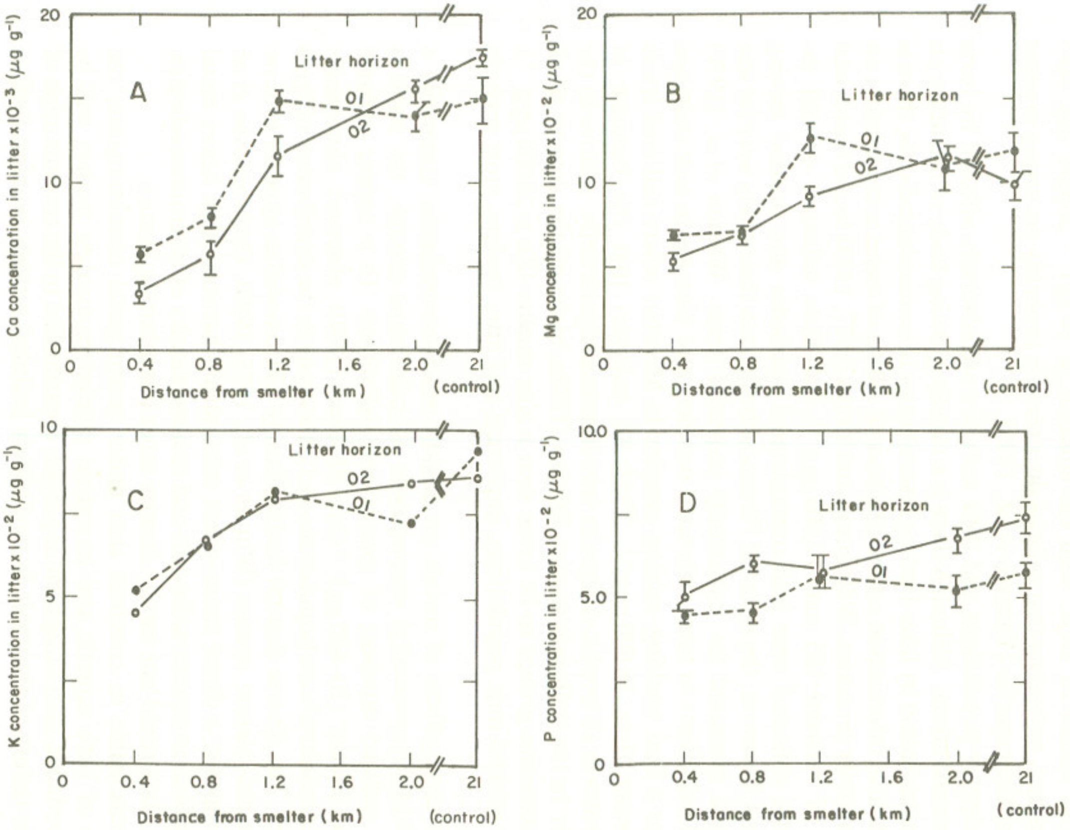

Figure 6.6 Macronutrient concentrations of (A) Ca, (B) Mg, (C) K, and (D) P(± 1 SE, $n = 12$) in forest floor litter as a function of distance from a lead smelter. (Reproduced from Jackson and Watson, 1977, *Journal of Environmental Quality*, volume 6, page 336, by permission of the American Society of Agronomy, Crop Science Society of America and the Soil Science Society of America)

carbon (DOC) from phytoplankton species. Wetzel (1975) suggested that membrane damage would increase the loss of DOC. Thomas *et al.* (1977) noted increased extracellular release with a copper concentration of 10–50 $\mu g\,l^{-1}$. A precipitous release of DOC with the addition of 50 $\mu g\,l^{-1}$ copper has been demonstrated, indicating that cellular disruption is probably occurring in some phytoplankton species (Vaccaro *et al.*, 1977).

Decomposer populations and their activities are adversely affected by toxic metal concentrations. Although there is a rapidly growing body of literature on metal accumulation by litter-feeding invertebrates in contaminated soils, there is little definitive information on the detrimental effects of metal accumulation on soil community processes. Williamson and Evans (1972, 1973) found that a lead content of between 165 and 19,000 $\mu g\,g^{-1}$ had little influence on soil invertebrates collected near lead-contaminated roadsides and around mining operations. However, the reported Pb concentrations in their study were far less than those measured for industrially impacted areas. Watson *et al.* (1976) reported reductions in total arthropod numbers and biomass in contaminated litter near a lead smelting–mining complex in Missouri where soil-lead levels were greater than 88 000 $\mu g\,g^{-1}$. Table 6.1 indicates that the biomass of invertebrates in all trophic categories was decreased significantly, relative to the proximity to the pollution source. Strojan (1978a, b) found the density of all major taxonomic groups to be lower near a zinc smelter ($Zn \geq 26\,000\,\mu g\,g^{-1}$), with the orbatid mite populations, important leaf litter feeders, most severely reduced.

The adverse effects of metals on aquatic macroinvertebrates (primarily a detritus-based community) encompasses all taxonomic groups; the trend is towards reduced numbers of species and individuals. In a copper-polluted mountain stream (20–630 $\mu g\,l^{-1}$ Cu), Sheehan (1980) observed abnormally small macroinvertebrate populations and alterations in the distribution of types of feeders. The diverse detrital feeding family Chironomidae appears to have several metal-tolerant species (Winner *et al.*, 1975, 1980). Occhiogrosso *et al.* (1979) proposed a direct cause–effect relationship between high heavy metal concentrations in aquatic sediments and reduced density of macroinvertebrates, although they could not totally dismiss other contributing factors.

It is reasonable to conclude that under severe metal contamination, the numbers of both aquatic and terrestrial detrital particulate feeders will be severely reduced, restricting their important contribution to the comminution of litter. The nature of their role in moderately polluted systems requires further investigation.

Excessive metal accumulation leads to a restructuring of microbial community composition. Jensen (1977) described the response of soil microbes to lead additions of 5000 $\mu g\,g^{-1}$ as reflecting a reduction in bacterial density with corresponding proliferation of a few tolerant fungal species. Metal-resistant fungal species found in zinc-contaminated soils appear to grow normally (Jordan

Table 6.1 Mean biomass of arthroped predators, detritivores and fungivores in litter from the 02 horizon on Crooked Creek Watershed ($n = 16$). (Reproduced from Jackson and Watson, 1977, *Journal of Environmental Quality*, volume 6, page 334, by permission of the American Society of Agronomy, Crop Science Society of America and Soil Science Society of America

Distance from smelter (km)	Biomass (mg m^{-2})		
	Predator	Detritivore	Fungivore
0.4	2.1[1]	2.3[1]	0.8[1]
0.8	5.8[1]	16.6[1]	2.4[1]
1.2	14.0	12.6[1]	5.8
2.0	87.6	92.6	16.1
21.0 (control)	17.3	61.1	22.1

[1] Significantly different from control ($P \leq 0.1$).

and Lechevalier, 1975). In addition, some zinc-tolerant actinomycetes and bacteria were present in the same soils, containing up to 13.5 per cent Zn in the upper horizon. Tolerant bacterial strains have been shown to display physiological characteristics different from those of sensitive species. The density of resistant strains has been shown to be inversely related to the level of metal concentration in the environment (Houba and Remacle, 1980). The work of Jordan and Lechevalier (1975) and Strojan (1978a) clearly indicated that both microflora and invertebrate activities in soil had been adversely affected near metal smelting operations, where concentrations of 900 μg g^{-1} Cd, 2300 μg g^{-1} Pb and 26,000 μg g^{-1} Zn in litter were 100 times greater than in samples from a control site. Jackson and Watson (1977) found significantly high C/N ratios in litter near smelters (where levels of 88 348 μg g^{-1} Pb, 128 μg g^{-1} Cd, 2189 μg g^{-1} Zn and 1315 μg g^{-1} Cu were 50 to 500 times those of control samples), indirectly indicating a reduction in microbial activity. The C/N ratio is inversely related to microbial population density (Witkamp, 1966). The microbial colonization of leaf litter in an artificial stream system was shown to be inhibited by relatively low levels of cadmium, 5 and 10 μg l^{-1} (Giesy, 1978). Reduced microbial colonization of litter has been shown to affect invertebrate feeding (Boling *et al.*, 1975). If these results can be applied generally, macroinvertebrates requiring leaf conditioning could be severely impacted at metal concentrations which inhibit microbial colonization but do not directly affect the feeding invertebrates.

Bond *et al.* (1976) found that Cd at 10 μg g^{-1} in a forest soil and litter microcosm reduced oxygen consumption and respiration by 40 per cent. A number of investigators have demonstrated reduced decomposition activity as measured by carbon dioxide evolution in artifically metal-amended soils (Ebregt and Boldewijn, 1977; Doelman and Haanstra, 1979a) and in contaminated litter-soil samples (Jackson and Watson, 1977 Chaney *et al.*, 1978; Strojan, 1978b).

Metal effects on soil enzyme activity indicate inhibition of essential reactions. Rühling and Tyler (1973) showed a highly significant negative correlation between total metal concentration (Zn + Cu + Cd + Ni) and dehydrogenase activity. Amylase activity in metal-contaminated litter was found to decrease linearly with the log concentration of total Cu + Zn + Pb + Cd (Ebregt and Boldewijn, 1977). A concentration of $1500\,\mu g\,g^{-1}$ Pb considerably increased the lag time to reach the peak rates of oxidation of starch and cellulose, and reduced the peak rates of oxidation of glucose, starch and glutamic acid, in soils (Doelman and Haanstra, 1979b). Tyler (1974, 1976) found a partial but immediate inhibition of phosphatase and urease enzymes due to copper and zinc salts, whereas β-glucosidase activity was not measureably affected. In Douglas fir needle litter, invertase activity was immediately inhibited and cellulase activity was depressed after four weeks, with treatments of $1000\,\mu g\,g^{-1}$ Hg or Cd (Spalding, 1979). Houba and Remacle (1980) noted that metal inhibition of certain essential enzymes may explain why metal-tolerant bacteria are unable to perform complete cellulolysis, pectinolysis or hydrolysis of starch under stressed conditions.

Whole-lake experiments with arsenic showed that seasonal influences mediate the impact of this pollutant on the microbial degradation of organic matter (Brunskill *et al.*, 1980). Under winter ice, $40\,\mu mol\,l^{-1}$ arsenate or arseniate inhibited degradation by 50 per cent, while during the ice-free season, there was little apparent effect on degradation rates.

The findings reviewed above lead to the conclusion that excess metal loading can significantly decrease the organic decomposition rate and consequently lead to increased litter accumulation. Rühling and Tyler (1973) concluded that even a moderate quantity of metal pollution would depress decomposition in Swedish forests. Strojan (1978a) observed progressively less weight loss from litter bags with increasing proximity to a zinc smelter and a significantly large ground accumulation of litter at 1 km from the smelter where levels of Zn, Pb and Cd were $26\,000\,\mu g\,g^{-1}$, $2300\,\mu g\,g^{-1}$, and $900\,\mu g\,g^{-1}$, respectively. For metal-tolerant vegetation, growing on metal mine wastes containing high concentrations of lead ($\sim 14,000\,\mu g\,g^{-1}$) and zinc ($400\,\mu g\,g^{-1}$), the rate of decomposition was retarded (Williams *et al.*, 1977). Even in less contaminated urban areas, black oak litter having levels of Pb from 33 to $305\,\mu g\,g^{-1}$ and Zn from 146 to $382\,\mu g\,g^{-1}$, decomposed at a slower rate than that on rural sites where metal concentrations were at least 75 per cent lower (Inman and Parker, 1978). Dixon *et al.* (1978) predicted that a 50 per cent increase in litter mass would occur in a simulated system with gross metal inputs, in less than six years. Jackson and Watson (1977) demonstrated an inverse distance–litter accumulation relationship near a lead smelter, as shown in Figure 6.7. Using regression analysis, Coughtrey *et al.* (1979) demonstrated that litter accumulation was highly dependent on cadmium levels and was associated with a particular size range of material (0.5–2 mm), suggesting that the effects occur during the later stages of breakdown. Reduced

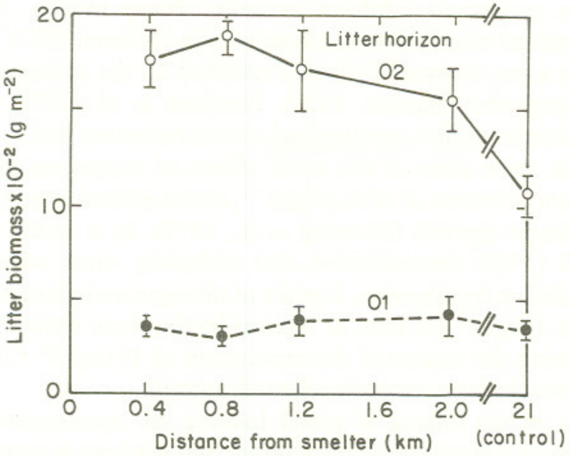

Figure 6.7 Biomass of forest floor litter ($\pm$ 1 SE, $n = 12$) as a function of distance from a lead smelter. (Reproduced from Jackson and Watson, 1977, *Journal of Environmental Quality*, volume 6, page 335, by permission of the American Society of Agronomy, Crop Science Society of America and the Soil Science Society of America)

leaf decomposition has also been demonstrated for a cadmium-stressed (5–10 μg l^{-1}) artificial stream (Giesy, 1978). The probable consequences of reduced litter decomposition on ecosystem function were summarized by Tyler (1972). Initially, some increase in soil litter occurs, with both the new fall and existing litter incompletely decomposed. This litter accretion can occur for only a limited time as more and more mineral nutrients become bound in forms unavailable to plants. The turnover of phosphorus, particularly, is retarded. Consequently, plant productivity decreases as does further litter fall. Even though litter mass is increased, concentrations of the macronutrients Ca, Mg, K and P are significantly depressed near metal smelters, probably as a result of an increase in acidic leaching accompanied by a decrease in microbial immobilization of these elements (Jackson and Watson, 1977).

As demonstrated for acid rain, excessive metal concentration interrupts the delicate ecosystem nitrogen cycle. Horne and Goldman (1974) observed the suppression of nitrogen fixation by blue-green algae with the addition of low levels of copper. They estimated that if ambient copper levels increased by 10 μg l^{-1} this could reduce the lake nitrogen budget by 40–50 per cent. Cadmium at 1.1 mg kg^{-1} has been shown to inhibit nitrogen fixation in Douglas fir needle litter (Lighthart, 1980). With increasing Ni levels, soil nitrification reactions were inhibited to a greater extent than were nitrogen and carbon mineralization (Giashuddin and Cornfield, 1978). Among the other heavy metals which are effective inhibitors are Hg, Cd and Cr (Liang and Tabatabai, 1978). Although zinc is not as potent an inhibitor as other heavy metals, $100\,\mu g\,g^{-1}$ Zn significantly reduced nitrification in amended soils (Wilson, 1977). The ammonification rate in some vineyard soils was retarded by the accumulated levels of copper-base fungicides (Baroux, 1972). Harrison *et al.* (1977) reported that inhibition of nitrate uptake, synthesis of nitrate reductase and loss of accumulated ammonia, were some of the acute effects of copper on phytoplankton. Copper, at a concentration of 10 to $25\,\mu g\,l^{-1}$, also inhibited uptake of silicic acid, essential to diatom growth (Goering *et al.*, 1977). In a series of microcosm studies, Heath (1979) demonstrated that cadmium stress adversely affected nutrient assimilation by microbes. Uptake of nitrogen and phosphorus occurred more slowly at $1\,mg\,l^{-1}$ Cd than at natural levels; these elements were barely assimilated during the course of the experiment at $10\,mg\,l^{-1}$ Cd. Phosphorus assimilation was the more severely affected process.

A summary of the effects of metal loading on decomposition processes includes numerous indications of disruption. Soil leaching is increased, and the decomposition rate decreased, contributing to an accumulation of nutrient-depleted litter.

6.2.3 Pesticides and Oils

Organic pesticides and oils cause a more specialized set of environmental disturbances than those discussed for either SO_2 or metals. The influence of these pollutants on decomposition processes and nutrient conservation has been less thoroughly investigated and, therefore, is more poorly defined.

Pesticides are used to restrict the numbers of certain undesirable species; however, because of their general lack of target specificity they can also reduce the populations of essential decomposer species, thus disrupting the balance within the decomposer community. Oil spills, essentially an aquatic problem, lead to severe impacts on nearshore marine ecosystems. The organic nature of these pollutants results in their providing additional organic energy to the affected system. This energy source can supply positive feedback to tolerant species, whereas sensitive and sometimes ecologically critical groups, such as those necessary for complete mineralization of normal litter, suffer extinction or reduction in numbers. Since there have been few studies on the influence of these pollutants on litter decomposition, the adverse effects of pesticides and oil spills are best surveyed through their direct impact on microbial and macroinvertebrate decomposers.

A comprehensive review of the impact of pesticides on soil fauna was presented by Edwards and Thompson (1973). These authors indicated that pesticides often affect nontarget species, many of which are saprophagous invertebrates (e.g. earthworms, Enchytraeid worms, Collembola, some mites and Diptera larvae) essential to the breakdown of leaf litter. Insecticides and nematicides are obviously toxic to many exposed soil and aquatic invertebrates.

Barrett (1968), examining the effects of the pesticide Sevin on a grassland ecosystem, reported that surface-dwelling invertebrates were reduced by 95 per cent in treated areas (2.5 $\mathrm{kg\,ha^{-1}}$ Sevin) and populations remained lower than control levels for more than 7 weeks. After 3 weeks, a significant reduction in litter decomposition rate was measured, presumably resulting from the earlier reduction in soil microarthropods and/or microbial decomposers. Brown (1978) reported that several carbamate pesticides (such as Sevin) were toxic to Collembola and mites at application levels of 1.4 to 11 $\mathrm{kg\,ha^{-1}}$, commonly used for gypsy moth control. Most pesticides were also highly toxic to the freshwater macroinvertebrate decomposer community. Sanders and Cope (1968) reported that of thirty-nine pesticides tested all but four had a 96-hour LC50 for stonefly nymphs, of less than 50 $\mu\mathrm{g\,l^{-1}}$, with the majority of LC50s less than 10 $\mu\mathrm{g\,l^{-1}}$. The spraying of organochlorines, organophosphates and carbamates for the control of forest pests (e.g. gypsy moths) has been found to have a severe impact on stream macroinvertebrates (reviewed by Brown, 1978).

There has been less research on the effects of oil on marine macro- and microinvertebrate decomposers. The activities of benthic deposit-feeders have been shown to be important in accelerating the degradation of sediment-bound oil (Gordon *et al.*, 1978). However Lindén *et al.* (1979) found that detrital feeding amphipods were reduced in oil spill areas, possibly through emigration as well as mortality. After ten months no significant recovery of amphipods was noted. As most other members of the soft-bottom community were also adversely impacted, it is difficult to imagine the litter-processing role of organisms like amphipods being successfully filled until the effects of the spill had subsided. Hampson and Moul (1978) reported that a fuel oil spill caused mortality of marine polychaetes, amphipods, decapods and isopods, and a significant reduction in faunal populations in marsh sediments was still evident three years later.

Although there is little information available, it has been noted that the effects of oils and pesticides on the microbial community deviate somewhat from those discussed for metals or acid rain. Pesticides and oils are toxic to certain microbial species. However, the most striking feature of microbial community response is the rapid population growth of those species directly involved in mineralization of the pollutant itself. Microbial responses to an oil spill are of two types: an inhibition of some naturally occuring groups of bacteria that may be critical in maintaining ecosystem balance and/or the development of a petroleum-degrading population that contributes to the removal of the oil (FAO, 1977). Growth-limiting effects of fuel oil No. 2 and Louisiana crude have been noted for ecologically important proteinolytic, cellulolytic, lypolytic and chitinolytic populations (Walker *et al.*, 1975). This study could have far-reaching implications relating to the completeness of litter decomposition which might be achieved under oil stress. Colwell *et al.* (1978) observed proportional decreases in starch hydrolysers and chitin digesters with parallel increases in petroleum

Table 6.2 Effect of *Metula* oil on representation of physiological groups of microorganisms comprising the heterotrophic populations of beach sand, given as per cent of the total viable count (*TVC*). Sd = standard deviation. (From Colwell *et al.*, 1978. Reproduced by permission of the *Journal of the Fisheries Research Board of Canada.*)

	Clean sand			Oil-impacted sand		
Physiological group	Mean % of TVC	No. of samples examined	sd	Mean % of TVC	No. of samples examined	sd
Starch	17.1	9	8.7	3.7	13	6.2
Chitin	6.6	19	8.1	1.8	15	1.6
Petroleum	0.018	17	0.043	0.050	19	0.145

degraders (Table 6.2). The altered balance was still evident 2 years after the *Metula* spill. Hodson *et al.* (1977) noted a reduction in microbial activity, as defined by glucose uptake, due to several crude and refined oils, an effect which could be interpreted as microbial switching from a natural substrate to oil.

Pesticide application appears to cause similar changes in soil microbial communities. Although reviews by Pfister (1972) and Tu and Miles (1976) indicated that halogenated pesticides and organophosphorous and carbamate insecticides did not significantly inhibit most microbial populations at normal application rates, certain pesticide compounds were selective for important decomposer groups such as fungi. Brown (1978) cited studies indicating that fungicides severely reduced fungi and nematodes, but often stimulated bacterial growth through elimination of competition and/or the utilization of dead fungi or the fungicide as an additional energy source. Mirex, at 100 $\mu g\,g^{-1}$ of soil, has also been shown to stimulate bacterial activity (Lue and de la Cruz, 1978). Fumigation of Douglas fir needle litter with a mixture of 98 per cent methyl bromide and 2 per cent chloropicrin caused increased microbial respiration (after a lag of nine days) which coincided with an increase in cellulase, xylanase, mannase and amylase activities (Spalding, 1979). Exposure of forest microcosm soils to 0.73 and 7.42 $mg\,cm^{-2}$ hexachlorobenzene (HCB), on the other hand, caused increased Ca loss and decreased CO_2 efflux (Ausmus *et al.*, 1979). Initial, rapid microbial decomposition of organic pollutants has been shown to deplete essential elements such as oxygen, nitrogen and phosphorus (Aminot, 1981), restricting subsequent mineralization rates due to nutrient limitations. The rates of mineralization of certain natural substrates (cellulose, chitin, starch,) may also suffer due to changes in the numbers and types of specialized decomposers, with pollutant degraders becoming dominant.

Overall, the rates of decomposition of soil litter in pesticide-polluted systems are generally lowered (Barrett, 1968; Perfect, 1979), the reduction of invertebrate activity being the most significant factor. The impact of oil on natural litter degradation remains undemonstrated in microcosm or ecosystem studies; a reduction in decomposition can only be inferred from the indirect evidence as presented above.

There is conflicting evidence also with regard to pesticide interference with nitrogen-cycling processes. A review of pesticide studies revealed that nitrogen fixation, ammonification and nitrification were mildly affected by pesticide residue concentrations, but that the severity of the impact was pesticide, soil-type and process dependent (Tu and Miles, 1976). Of these processes, nitrification appeared to be the most sensitive to initial exposure. Winteringham (1977) indicated that nitrification showed more sensitivity than ammonification to organochlorines such as DDT. Reduction in root nodules has been demonstrated for DDT at 100 kg ha^{-1}. Herbicides such as PCP and DNOC decrease introgen fixation by *Azotobacter*, and phenoxy herbicides can suppress legume nodulation (Brown, 1978). Pentachlorophenate, at concentrations of 100 $\mu g\,g^{-1}$ and above, strongly inhibited N-fixation in soils (Tam and Trevors, 1981). In addition, PCP was found to decrease ammonification, while most other herbicides increased the formation of NH_4–N.

The importance of such disruptions to the availability of nitrogen to primary producers has not been clearly demonstrated. It is suggested that inhibition of nitrogen fixation could be particularly critical in nutrient-deficient natural ecosystems. Shindler *et al.* (1975) hypothesized that *Azotobacter* species were stimulated to fix atmospheric nitrogen in oil-polluted freshwater ponds, thereby contributing to the heightened N/P ratio observed, in comparison to unpolluted controls.

There is no evidence that oils or pesticides promote direct leaching of nutrients from soils or sediments as previously noted for metals and acid rain. However, in cases of severe exposure, nutrient export and increased erosion have occurred. Likens and Bormann (1975) reported that herbicides reinforced the already established trend of nitrate loss from felled vegetation. Pesticides may also accelerate nitrogen loss in agricultural systems (Winteringham, 1980). In the absence of active plant uptake, the very mobile nitrate is flushed from the ecosystem. Woodwell (1970) theorized that herbicides cause ‘leaks’ in the nutrient conservation system, presumably through elimination of biomass storage capacity. Perfect (1979) and Perfect *et al.* (1979) suggested that there was a link between DDT interference with nutrient cycling and subsequent decreased crop yield in agro-ecosystems, although they were unable to establish the exact nature of this disruption. Hampson and Moul (1978) showed that erosion of marsh soils was increased by the long-term damaging effects of fuel oil on the marsh vegetation. After 3 years they found that erosion rates were 24 times greater than those measured at an undisturbed control site. The increase correlated well with the degeneration of the intertidal marsh root system which normally acts as a sediment-binding mechanism. Zeiman (1975) concluded that the denuding effect of oils on sea-grass systems led to increased erosion and that oil,

Table 6.3 Summary of pollutant effects on decomposition processes and element conservation in ecosystems

	Decomposer organisms		Litter accum-lation	Litter decomposition rate	Leaching	Nutrient export	Nitrogen cycling	
Pollutant	Invertebrates	Microbes					N_2-fixation	NO_2, NO_3
Acid precipitation	Decreased	Decreased; favoured fungi	(+)	Decreased	Increased soil and foliar loss	Accelerated net loss	Decreased	Decreased
Heavy metals	Decreased	Decreased; may favour fungi	(+)	Decreased	Increased soil loss	Accelerated net loss	Decreased	Decreased
Pesticides	Decreased	Species composition changes favouring pollutant-mineralizing species at the expense of ecologically important groups; fungicides are particularly harmful to fungi	(+)	Decreased	Effects unknown; herbicides can stimulate vegetative release of dissolved organics; HCB induced Ca leaching	Accelerated net loss particularly with herbicides	No effect?	Decreased?

Oil	Decreased	Species composition changes favouring oil mineralizers; possible decrease in the proportion of chitin and starch degraders	(?)	Effects unknown; rates assumed to be depressed; decomposition may be at some point nutrient limited	Effects unknown	Erosion has been demonstrated for Marsh Grass systems	Possibly stimulated in some cases	Effects unknown

coating the sediment, inhibited rapid recolonization, thereby accelerating the erosion process.

Although there are some obvious differences in the effects of each pollutant discussed, on decomposition subsystems, a summary of their effects on component organisms and selected decompostion processes shows that there is some similarity in ecosystem response (Table 6.3). The rate of invertebrate comminution of litter is often drastically reduced as is the general rate of litter decomposition. Material export, resulting from leaching of inorganic nutrients or from general soil erosion, is associated with pollution loading at subacute levels and is accelerated with acute long-term or gross exposure. Inhibition of conservative nitrogen cycling has frequently been found to occur, with the nitrification process being particularly sensitive. The similarities among decomposer subsystem responses to pollution strongly suggest the feasibility of using decomposition and element cycling criteria to measure pollution stress at the ecosystem level. This approach should be particularly effective in cases of terrestrial and flowing-water systems, where a large fraction of the organic matter is processed as detrital material.

6.3 PRODUCTIVITY AND RESPIRATION

Solar radiation is the ultimate source of energy for the living system; however, it must be concentrated and stored by the photosynthetic process. This process is the critical link in the energy base, fundamental to both autotrophic maintenance and heterotrophic development. Inhibition of photosynthesis due to pollution stops ecosystem energy movement at this most critical initial conversion. The impact of a toxic pollutant on photosynthesis may be effected through death of the plant or necrosis of photosynthetic tissue, through direct inhibition of photosynthetic reactions, or through indirect rate limitation brought about by a pollutant's effect on the availability of essential elements for plant growth.

The primary result of partial inhibition of photosynthesis is a progressive reduction in the size of the available energy pool, and an increase in the turnover time in which the pool is replenished. This decrease in gross primary production, even if accompanied by an equivalent reduction in autotrophic respiration, will still significantly diminish net primary production. This would mean that less energy would be available to heterotrophs. Since pollutant stress often, in fact, increases total ecosystem respiration while decreasing productivity, the available energy pool could be even further reduced. A diminished net energy reservoir is often accompanied by a reduction in species variety. A simplified plant community can mean reduced availability of preferred species and changes in the digestibility and nutrition of available food. The availability of essential 'quality' energy to heterotrophs then, is subject to the additional constraint of changed nutritional value.

Another aspect of primary productivity is the relationship of the pollutantgenerated perturbation to the seasonality of ecosystem growth. The terrestrial plant community is most sensitive to stress during certain vegetative stages (germination and bud formation). Exposure to toxic substances during these critical phases enhances the potential for plant damage. Other pollutant-sensitive factors governing plant growth such as nutrient availability and grazing pressure are often correlated with seasonality, as well. Hunding and Lange (1978) stated that the developmental stage and physiological states of individual species must be considered in the study of ecotoxicology of aquatic plant communities. The vulnerability of terrestrial productivity to pollution stress is also influenced by the stage of successional development of the ecosystem. Vitousek and Reiners (1975) argued that in the course of succession, element outputs are initially high, that they later drop to a minimum due to accumulation in biomass and detritus when net ecosystem production is highest and that, eventually, outputs rise to balance inputs. Therefore, late successional plants are less well adapted to conditions of nutrient flux which often accompany pollutant disturbances than are species from the early colonizing community.

Smith (1974) divided the impact of pollutants on plants into three major classes based on the severity of response. A class I response represents low pollutant loading with the plant community acting as a sink for the contaminants. This type of response is subtle and can only be estimated through chemical extraction techniques; however, it often provides the initial evidence of pollutant accumulation and movement from the abiotic to biotic components of the ecosystem. Class II responses are found with intermediate pollutant loading. At this stage, plants show reduced growth, reduced reproduction and increased morbidity of individual species, leading to reduced productivity and biomass, altered species composition and increased vulnerability at the ecosystem level. This set of reactions is based primarily upon extrapolation of controlled laboratory and small field experiments with limited microcosm and ecosystem data. Class III responses represent acute damage to the plant community; resultant simplifications in the biotic structure of the ecosystem infer reduced stability. Extensive acute damage is readily observable in the field.

The development of an understanding of ecosystems functioning at the class II response level is of particular interest to ecotoxicologists since the reduced 'health' of the system can often be reversed if correct diagnosis leads to decreased contamination.

6.3.1 Acid Rain

There are a variety of experimental studies demonstrating that air pollutants such as acid precipitation reduce photosynthetic rate, plant growth and reproductive success, and consequently reduced plant yield. Bennett and Hill (1974) demonstrated that chronic exposure of plants to a number of phytotoxic air pollutants (HF, Cl_2, O_3, SO_2, NO_2, NO) can cause a reversible suppression of photosynthesis. Of the phytotoxic air pollutants tested, combinations of SO_2-NO_2, major constituents of acid rain and ozone, are the most likely to occur in the ambient atmosphere in sufficiently high concentrations to depress this process. Bennett and Hill concluded that although plants generally recover from recurring episodes of short-term pollutant exposure, when sufficient recovery time is allowed, it is probable that prolonged exposure chronically depresses photosynthesis, leading to visible symptoms of injury and reduced growth.

Much of what we know of the effects of SO_2 on primary producers has come from lichen investigations. Although the aim of much of this research has been to discover why this unique group is sensitive to SO_2, it has produced some general understanding of the mechanisms of SO_2 damage to plants and of their ability to recover under various stress conditions. With short-term exposure, lichens are no more sensitive to SO_2 than are higher plants; however, they have the ability to efficiently absorb the pollutant, accounting for their disappearance from contaminated areas (Nash, 1973). Lichens are more sensitive to sulphur in simulated acid rain than in its dry forms (Türk *et al.*, 1974). There is a very rapid (within 15 minutes) decrease in photosynthetic ^{14}C fixation with exposure to aqueous sulphur dioxide, and repeat exposures reduce the plants' ability to recover a normal photosynthetic rate (Puckett *et al.*, 1974). After a slight increase in photosynthesis at low SO_2 concentrations, the reduction in photosynthetic ^{14}C fixation becomes pronounced with lower pH and increased sulphur dioxide concentrations, as shown in Figure 6.8 (Nieboer *et al.*, 1976). Tomassini *et al.* (1977) demonstrated that the per cent total ^{14}C fixation decreased expontially with increasing concentrations of SO_2 at gross exposure levels with short exposure time. The fixation rate–exposure time relationship became linear with low level exposure for 6 to 12 hours. Through extrapolation, they estimated the injury threshold concentration of SO_2 as acid precipitation for the lichen *Cladonia rangiferina* to be $10\,\mu g\,l^{-1}$ for six months.

Researchers have found that limited exposure to SO_2 not only reduces gross carbon assimilation but also influences metabolic expenditures. Respiration rates were depressed during incubation in sulphur dioxide solutions (Baddeley *et al.*, 1973; Tomassini *et al.*, 1977). Differences in lichen respiratory response which are not specifically related to SO_2 concentration may be due to differences in the sensitivity of the fungal partner; however, the algal symbiont has been shown to be the more sensitive to SO_2. In fact, Hällgren and Huss (1975) showed that the nitrogen-fixing capability of lichens and blue-green algae was more sensitive than their photosynthetic capacity to SO_2 exposure. Thus, SO_2 pollution has very complex metabolic effects on the exposed lichen, effects which either directly or indirectly reduce its productive capacity.

The foliar efflux of potassium ions and the bleaching of pigment have been found to result from extended SO_2 exposure, and these injurious effects culminate in permanent reduction of net photosynthesis and, presumably, permanent impairment of the lichen (Nieboer *et al.* 1976). Excessive foliar

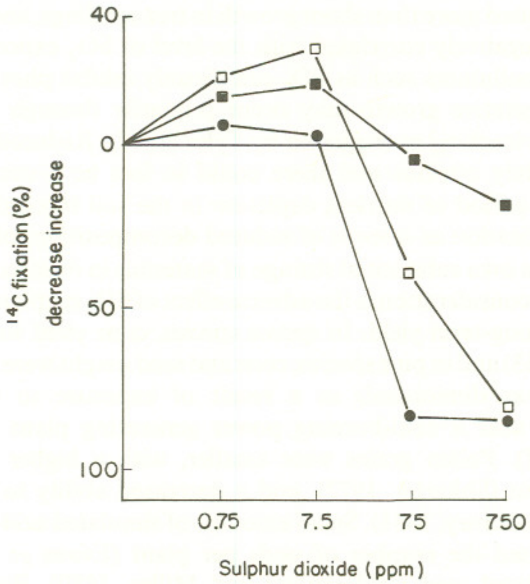

Figure 6.8 The percentage reduction in net ^{14}C fixation by *Stereocaulon paschale*, incubated for 6 h in solutions of sulphur dioxide buffered at various pH values, as compared with control samples without sulphur dioxide. Each point represents the mean of six replicates. ■ pH 6.6; □ pH 4.4; ● pH 3.2. (Reproduced with permission from Nieboer *et al.*, 1976. In Mansfield, *Effect of Air Pollutants on Plants*, Cambridge University Press)

leaching represents severe disruption of the plant community and infers photosynthetic impairment on a broad scale.

Feder (1973) noted that the line of reasoning developed from SO_2-lichen studies may be quite applicable to much of the terrestrial plant community. He indicated that the hidden injuries to plants from chronic exposure are reflected in reduced photosynthesis, decreased growth, and fast aging of foliage, which cumulatively result in reduced system viability and yield. Increased transpiration and dark respiration resulting from exposure to elevated SO_2 levels of > 3.5 mg m^{-3}, for the initial few days, constitute heightened metabolic expenditures (Ziegler, 1975) and consequently reduce productivity. Recent work by Constantinidou and Kozlowski (1979a, b) revealed additional indirect evidence of SO_2-induced loss in primary productivity as measured by the following parameters: (1) diminished leaf expansion, (2) fewer emerging leaves, (3) a decrease in total non-structural proteins and carbohydrates in new leaves, (4) reduction in root weight. Marshall and Furnier (1981) reported that root growth was inhibited more than shoot growth in tree seedlings, and the reduction in growth was negatively correlated with the level of SO_2 exposure.

Although air pollutants such as SO_2 can directly inhibit photosynthesis, the reduction of vegetative growth may occur primarily through stimulation of essential element leaching as suggested by Tyler (1972). Reduced growth might not be immediately obvious and there could in fact be a substantial delay, encompassing a period of nutrient depletion in the soil through leaching and element immobilization as a result of reduced decomposition, plus draw-down time for the tree's own substantial storage of materials in its structural biomass.

An additional consideration is the adverse effect of SO_2 on plant reproduction with respect to long-term yield. In spruce species, cone yield was shown to be smaller (Pelz, 1963) and in pine species, cone and seed weight were decreased, and seed viability was diminished, as a result of exposure to 0.06 mg SO_4^{2-} cm^{-2} $month^{-1}$, near a coal-burning power generating plant (Houston and Dochinger, 1977). Pollen grains were smaller, with a higher proportion of underdevelopment (Shkarlet, 1972), and a decreased ability to develop tubes (Varshney and Varshney, 1981). Small amounts of simulated acid rain applied to soybeans decreased the number of pods per plant (Evans *et al.*, 1980) and significantly reduced seed yield (Irving and Miller, 1980). Possible harmful influences of acid precipitation on germination and seedling establishment in mineral soils have been pointed out as well (Teigen, 1975; Abrahamsen *et al.*, 1977). About 80 per cent of Norway spruce and Scots pine seeds did not develop normal seedlings at pH 3.8 (Teigen, 1975).

Although there is considerable evidence of SO_2-induced reductions in the short-term growth rates of plants potentially affecting agricultural yields (e.g. Reich *et al.*, 1982), long-term reductions have not been as clearly demonstrated. However, in a forested area surrounding a 'sour gas' processing plant, sulphur emissions reduced the woody production of hybrid lodgepole × jack pines (Figure 6.9). The maximum depression of basal area incrementation occurred at sites approximately 1 and 3 km from the gas plant and decreased to minimal or no effect at a distance of 9.6 km. A difference of approximately 2 per cent in basal area growth was evident between trees at 1 and 9.6 km over a 14 year period following the start-up of the gas plant (Legge, 1980). Results of field experiments using artificial acid rain as the treatment on Norway spruce and Scots pine showed that growth effects were most obvious at pH 2.0 and 2.5 (Tveite, 1980; Tveite and Abrahamsen, 1980). Growth in height of Scots pines showed an increase with acid rain treatment during a 4-year period. Tveite and Abrahamsen (1980) suggested that the stimulated growth was probably the result of increased nitrogen or sulphur availability, or both. On the other hand, in the Norway spruce stand, height and girth growth were reduced by the low pH treatments (Tveite, 1980). A regional tree-ring study in Norway also yielded inconsistent growth results associated with acid precipitation (Abrahamsen *et al.*, 1976). The conference summary from the recent SNSF international meeting on the

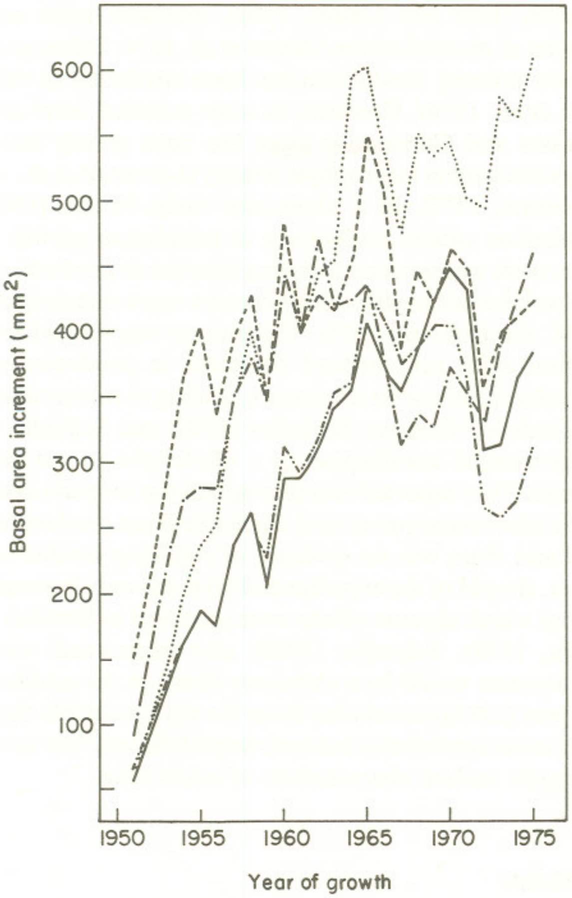

Figure 6.9 Comparative plots of the mean basal area increments from lodgepole x jack pine trees at each of five ecologically analogous sampling sites approximately 1.2 (——), 2.8 (——..——), 6.0 (——.——), 7.6 (----) and 9.6 (.....) km, respectively, from a 'sour gas' processing plant source of sulphur gas emissions. (Modified from Legge, 1980. Reproduced by permission of USDA Forest Service)

ecological impacts of acid precipitation stated that it was not yet possible to draw a definitive conclusion on the effects of acidification on forest growth, although induced deficiencies of K, Ca and Mg may have long-term effects on productivity (Last *et al.*, 1980).

Some of the symptoms of reduced productivity have been noted for aquatic systems although the primary producer response is less clear. Production at the macro- and microconsumer levels was reduced by experimental acidification of a stream ecosystem (Hall and Likens, 1980). Acidified lakes are reported to have fewer species of phytoplankton (Almer *et al.*, 1974; Dillon *et al.*, 1979; Yan, 1979), and lower primary production has been attributed to reduced nutrient supply (Grahn *et al.*, 1974). However, in some acidified lakes and streams the growth of mosses and filamentous algae has been greatly increased, with a corresponding reduction in macrophyte density (Leivestad *et al.*, 1976; Hendrey *et al.*, 1976; Grahn, 1977). In a whole-lake study, Müller (1980) found that artificial acidification caused an increase in periphyton growth in the littoral zone; however, there was no corresponding increase in productivity. It has been suggested that as lakes are acidified they become more oligotrophic (Grahn and Hultberg, 1974; Grahn *et al.*, 1974). The process was termed self-accelerating oligotrophication since acid-induced decreases in productivity could cause starvation or reduced 'fitness' in consumers, leading to further disruptions of the food web and reduced biomass. Schindler (1980) and Schindler *et al.* (1980a) conducted experimental acidification of a whole lake to test the oligotrophication hypothesis. They reported that phytoplankton biomass and chlorophyll *a* increased as the lake became more acid. Phytoplankton production per unit area also increased and there was no evidence of declining production in the food chain. However, the pH in the experimental lake was only lowered to 5.6, above the value of 5 at which chronic effects were observed in Swedish lakes (Wright and Henriksen, 1978). Schindler (1980) also questioned whether primary productivity increases would be a transitory phase in the acidification process. An NRCC report (1981a) concluded from the data available that productivity did not appear to be significantly reduced despite the very low concentrations of dissolved inorganic carbon characteristic of acidic lakes.

6.3.2 Heavy Metals

Contrary to the reports of direct SO_2 effects on photosynthesis in terrestrial plants, there is little information indicating that metals directly affect the photosynthetic process (Foy *et al.*, 1978). However, the end result of medium to high levels of heavy metal pollution appears to be reduced primary production. Cupric ions have been shown to inhibit photosynthetic electron transport in isolated chloroplasts, but this effect has not been demonstrated in whole-plant studies (Cedeno-Maldonado *et al.*, 1972). Reductions in ^{14}C fixation can be induced by a number of heavy metals (Ni, Cu, Zn, Pb) in both algal cultures and natural phytoplankton populations (Erickson, 1972; Bartlett *et al.*, 1974; Steemann Nielsen and Bruun Laursen, 1976). It has been suggested that lead may inhibit plant growth near major highways (Coello *et al.*, 1974). It is possible that where heavy metals have reduced terrestrial plant productivity, the effects may have been indirect and may have been manifested through reduction of photosynthetic surfaces, inhibition of metabolic enzyme systems or interference with nutrient uptake. Furthermore, damage to a forest ecosystem, due to other stresses such as fire, is aggravated by high metal levels. Toxic metals apparently inhibit seed production, preventing vegetative reestablishment.

The most general symptoms of excessive metal levels are stunting and chlorosis. The latter represents tissue injury and may be due to an iron deficiency caused by competitive interaction with multivalent heavy metal ions. Chlorosis from excess Zn, Cu, Ni and Cd appears to be due to direct or indirect interaction with foliar Fe. This symptom is aggravated by low pH and iron-depleted soils (Foy *et al.*, 1978). White *et al.* (1974) observed that excessive zinc may also increase manganese transport levels in plant tops, interfering with chlorophyll synthesis. Inhibition of enzyme activity has long been cited as a major biochemical mechanism associated with metal toxity. Competitive inhibition of metalloenzymes may be of particular importance. Increased metabolic costs and indirect reduction of photosynthetic capability would eventually lead to reductions in whole-plant growth. Stunting can result from the interaction of several factors including specific toxicity, antagonism with nutrients and inhibition of root penetration and growth.

Toxicity is first evident in root tips, followed by subsequent inhibition of lateral root development, resulting in uptake of phosphorous, potassium and iron at rates insufficient for normal growth (Barber, 1974). Whitby and Hutchinson (1974) demonstrated a relative reduction of root elongation by tomato plants in solutions of nickel, copper, cobalt and aluminium, between 2–10 $\mathrm{mg\,l^{-1}}$. They noted this as significant because water extracts often yield levels in excess of 10 $\mathrm{mg\,l^{-1}}$ in soils from contaminated areas. Plants grown in soil-water extracts taken from sites closer than 3.8 km to a smelter (Sudbury) showed almost total inhibition of radicle elongation. At distances of 3.8 to 10.4 km, root growth, when compared with that of controls, was found to be related to proximity to the smelter and corresponding concentrations of Ni, Cu, Al and Zn. Observers noted a depletion in fine roots in litter polluted by lead smelter emissions (30 000–88 000 $\mu\mathrm{g\,g^{-1}}$ Pb), and found extremely high concentrations of heavy metals in root tissues (Jackson and Watson, 1977). Seedlings in zinc-contaminated soils, collected near a smelter operation, produced significantly less root and shoot growth than did controls: Figure 6.10 (Jordan, 1975). Presumably, inhibition of decomposition and elevation of soil nutrient leaching by metals would aggravate any difficulty in the uptake of essential elements by unhealthy roots. Jackson and Watson (1977) found depressed nutrient concentrations in leaf tissue sampled from plants near a lead smelter. It might require several years of inadequate nutrient uptake before such a deficiency becomes noticeable in plant leaves (O'Neill *et al.*, 1977; Jackson *et al.*, 1978). Reduced nutrient levels in leaves should be considered as indirect evidence of a corresponding reduction in structural growth.

Tyler (1972) suggested that metal-retarded mineralization of litter, with subsequent reductions in the availability of nutrients, contributes to reduced

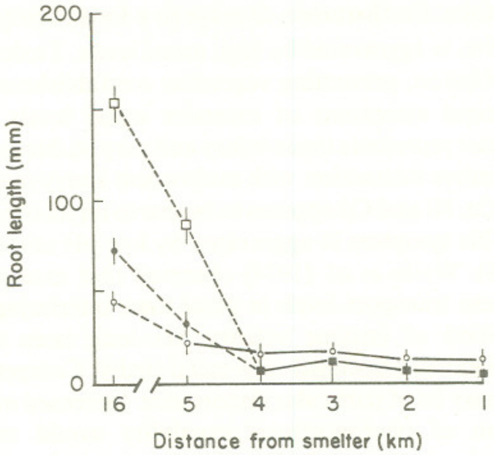

Figure 6.10 Root length of *Quercus rubra* seedlings germinated on soils collected various distances from a metal smelter. Means ± SE are plotted. Open circles indicate 42 days, closed circles 60 days, and squares 69 days growth. Means differing significantly at the $P \leq 0.05$ level are connected by dashed lines. (From Jordan, 1975. Copyright © 1975 Ecological Society of America)

ecosystem productivity. This series of events may act as a self-stimulating cycle. If pollutant loading were continued, the cycle could only be reversed through the genetic adjustment of organisms at all important links in the decomposition chain. Bradshaw *et al.* (1978) indicated that restoration of vegetation on metal mining waste required application of organic matter, to reduce direct metal toxicity through adsorption and chelation, and fertilizers containing N, Ca, P, K and Mg, to overcome very depressed nutrient levels in the soils.

Although cases of excessive metal concentrations in soils or irrigation water reducing crop productivity have been documented (Huisingh, 1974; Bingham *et al.*, 1980), there are few examples of long-term reductions in productivity in nonagricultural ecosystems. Rather, it is thought that for forested systems, a gradual reduction in plant growth does occur but is not easily quantifiable (Hughes *et al.*, 1980b). Hutchinson and Whitby (1974, 1977) reported a considerable reduction in forest productivity due to a combination of SO_2 acidity and metals.

Reduction of net primary productivity and phytoplankton biomass due to metal contamination has been observed more frequently in aquatic systems, where the producers' small size and rapid turnover rate elicit a more rapid response to perturbation and facilitate productivity measurements. The microcosm studies by Gächter and Máres (1979) demonstrated that an initial combined loading of heavy metals ($\leq 1\,\mu g\,l^{-1}$ Hg, 5–7 $\mu g\,l^{-1}$ Cu, 2–3 $\mu g\,l^{-1}$ Cd, 98–196 $\mu g\,l^{-1}$ Zn and 4–8 $\mu g\,l^{-1}$ Pb) lowered phytoplankton biomass as well as species number and photosynthetic activity. Comparable results have been reported for single additions of 10 to 50 $\mu g\,l^{-1}$ copper (Thomas *et al.*, 1977; Harrison *et al.*, 1977). Levels of copper as low as 5 to 10 $\mu g\,l^{-1}$ affect algal growth, indirectly, through inhibition of nitrogen fixation (Horne and Goldman, 1974), and at 25 $\mu g\,l^{-1}$, through interference with silicic acid uptake by diatoms (Goering *et al.*, 1977). Mercury, at levels greater than 30 $\mu g\,l^{-1}$, lowers the rate of algal cell division and induces cellular losses of nitrogen and lipids (Sick and Windom, 1975). Growth of *Selanastrus capricornutum* was inhibited in assays with contaminated Coeur d'Alene River water containing Zn levels greater than 0.5 $mg\,l^{-1}$ (Bartelett *et al.*, 1974). In a further study of heavy-metal effects, Wissmar (1972) reported that in the highly polluted Coeur d'Alene Lake, the combined effects of Zn, Cu and Cd reduced carbon fixation by lake phytoplankton.

Aquatic microcosm studies have shown that toxic metal levels affect the ratio of gross primary production (*GPP* or often termed simply *P*) to total ecosystem respiration (*R*). Odum (1956) proposed the use of the P/R ratio to classify systems as autotrophic ($P/R > 1$) or heterotropic ($P/R < 1$), and suggested that mature aquatic ecosystems tend to approach a P/R ratio of 1. This approximate value has been measured in a whole-lake ecosystem (Jordan and Likens, 1975). With the addition of 11.5 $mg\,l^{-1}$ arsenic to microcosms, P/R dropped to nearly zero and did not recover for 2 weeks (Giddings and Eddlemon, 1978). An input of 10 $mg\,l^{-1}$ cadmium (Heath, 1979) or 0.5 $mg\,l^{-1}$ copper (Whitworth and Lane, 1969) significantly depressed P/R in similar microcosm studies. A ratio of less than 1 would indicate a negative energy balance which could be detrimental if allochthonous sources were unavailable or the system was unable to recover rapidly. However, Fisher and Likens (1973) found $P/R < 1$ for streams and argued that most mature aquatic ecosystems would be heterotrophic and open to allochthonous inputs. The applicability of the P/R ratio in evaluating stress would be doubtful for ecosystems that were already primarily heterotrophic ($P/R < 1$).

Evidence of loss of net productivity at intermediate levels of metal stress is substantially lacking for forested ecosystems although a good case for its existence has been argued. Metal-induced depression of productivity most certainly occurs and may persist in polluted aquatic systems; therefore, its use as a dynamic measure of ecosystem response to metal stress should be encouraged.

6.3.3 Pesticides and Oils

Generalizations concerning the response of the primary production processes to either pesticides or oil pollution are nearly impossible. Productivity is either stimulated or depressed depending on the type of pesticide or oil, as well as its concentration, and a number of other factors.

Herbicides in general are quite disruptive to production processes and cause widespread mortality. The product 2,4-D applied to Colorado rangeland reduced forbes on a fairly permanent basis. Use of 2,4-D and 2,4,5-T in Vietnam showed that a double spraying of 28 kg ha^{-1} would reduce triple canopy forest to a grass–sedge system quite rapidly (in Brown, 1978).

Pesticides are often applied to increase crop yield through the reduction of pest species. However, continuous application under nonagricultural conditions (without fertilizer addition) has led to an eventual decrease in productivity (Perfect, 1979; Perfect *et al.*, 1979). It has been shown that DDT-treated plots had higher plant yield than untreated plots for the first few years of application, after which the trend reversed, and the decline in the rate of yield as function of time was accelerated in the treated plots. The reduction in yield was associated with DDT's effects on soil biota and nutrient cycling processes.

Organochlorines generally reduce photosynthesis in aquatic ecosystems (Wurster, 1968; Johannes, 1975), although 0.02 mg l^{-1} DDT did not significantly depress P/R in artificial pool studies (Whitworth and Lane, 1969). A stream ecosystem demonstrated the capacity to adjust P/R rapidly in response to 9 mg l^{-1} of the lampricide TMF (Maki and johnson, 1976). Organophosphorous compounds often stimulate primary productivity either through addition of phosphorous or through reducing grazing pressure (Butcher *et al.*, 1975, 1977). Increases in photosynthetic activity were found to correlate with levels of pesticide application, giving additional evidence of the phenomenon of nutrient stimulation.

Very few studies have been made of oil-pollution effects on terrestrial ecosystems. An oil spill in a grass–herb community was found to reduce total plant production by 74 per cent over a 6-month period (Kinako, 1981). The inhibitory effects of oils on the aquatic plant community are most obvious for rooted species. Marsh grasses have been shown to be severely reduced by No. 2 fuel oil, and recovery of the community either through reseeding or rhizome growth was hampered (Hampson and Moul, 1978). Baker (1971) found that the recovery of salt marsh grass was reduced by successive spills. Hanna *et al.* (1975) showed that freshwater macrophytes were greatly reduced in arctic lakes under oil stress, although the productivity of the lakes was not significantly reduced. This finding infers that perhaps phytoplankton are stimulated by the addition of oil. Algal blooms have been reported after major oil spills (Lindén *et al.*, 1979; Johansson *et al.*, 1980); the investigators hypothesized that reduced grazing pressure was the primary reason for these blooms. Shindler *et al.* (1975) suggested that nitrogen fixation might be stimulated by oil in freshwater systems, also contributing to increased productivity. Short-term exposure to No. 2 fuel oil at 1.2 to 15.3 mg hydrocarbon l^{-1}, however, depressed photosynthetic activity and phytoplankton biomass in *Vaucheria* (Bott and Rogenmuser, 1978). The general consensus emerging from oil pollution research on pelagic systems is that although natural phytoplankton communities are sometimes adversely affected by oil, the organisms are sufficiently prolific that individual oil spills will have only transitory effects on overall community productivity (FAO, 1977).

The redundancy existing in the functional and regulatory processes of ecosystems, and the large stored biomass inherent in forest systems, tend to mask short-term pollutant effects on the producer communities. Long-term studies of acid precipitation effects on forests and of the influence of metals on productivity adjacent to smelter operations may clarify our understanding of the effects of pollution on long-term energy processing.

6.4 FOOD WEB AND FUNCTIONAL REGULATION

One of the most poorly understood yet important features of ecosystem function is the role that consumer organisms play in regulating energy and nutrient dynamics. Owen and Weigert (1976) suggested that the mutualistic relationship between some plants and their consumers promotes maximum fitness in the plants. The important role of herbivores in recirculating nutrients contributes to an ecosystem's resilience to perturbations (Webster *et al.*, 1975).

The consumer complex acts to control the producer and decomposer components of the system (Golley, 1973). Predator and parasite populations are limited by the reductions in energy as it passes through the food chain and by the availability of essential materials. Thus, there are physical and chemical limits to the length of the food chain, and any further trophic elaboration is biologically regulated. This control can be achieved through a variety of competitive and trophic interactions and through the feedback from specific interdependent relationships.

Golley *et al.* (1975) grouped the various impacts of regulators into categories relating to : (1) destruction of a component by organisms, (2) the movement of materials, (3) alteration of the environment, (4) interactions with other consumers, particularly predators. Each of these categories involves direct effects on biological components and on the rates of transfer of energy and materials between components. These impacts may have hierarchical and indirect effects on many components within the system at the same time. Also, they can change the abiotic environment.

The role of consumers in functionally regulating ecosystems has been most frequently discussed in terms of energy flow (see Teal, 1957; Fisher and Likens, 1973; Reichle *et al.*, 1973a, b). The impact of consumer regulation on energy movement has been generally assumed to be equivalent to the magnitude of energy flowing through the population. For example, the effect of phytophagous insects on forest production was related to their consumption of foliage (Rafes, 1970; Mattson and Addy, 1975). Cummins (1974) associated energy processing in a heterotrophic stream with the breakdown of leaf litter, thereby accounting in part for the flow of both energy and nutrient materials.

More recently, analysis of consumer regulation of nutrient cycles through

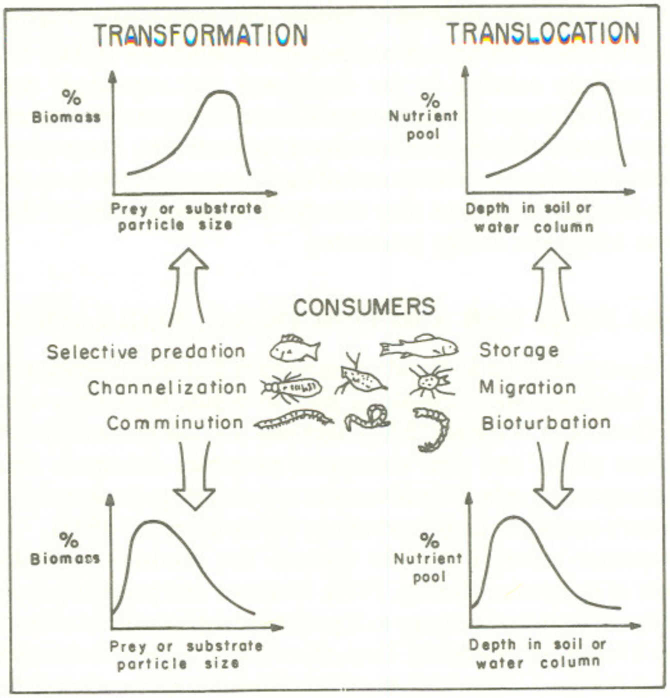

Figure 6.11 Graphic representation of consumer effects on nutrient cycling processes in ecosystems. Translocation or redistribution of nutrients occurs when mobile consumers cross subsystem boundaries. (From Kitchell *et al.*, 1979. Copyright © American Institute of Biological Sciences)

processes not directly reflected in energy flow has been proposed. Kitchell *et al.* (1979) suggested that regulation at the physico-chemical level occurs through consumer impact on translocation and transformation processes. Consumer effects on the cycling process are summarized in Figure 6.11. Translocation processes would include migration, storage in biomass, bioturbation (mixing of sediments) and movement of litter and faeces within the system. Transformation processes would include selective predation, the comminution or agglutination of litter particles and chemical transformation of substrates. Translocation by mobile consumers redistributes nutrients, retards their loss to soils and sediment and facilitates nutrient availability for primary producers, particularly during critical growth periods, through control of the rate of excretion. Transformation of the size of organic units alters cycling rates through changes in surface–volume relationships. Nutrient pools composed of large biomass units (e.g. tree stumps, leaf litter) may be broken into smaller units, increasing nutrient release. On the other hand, nutrients may be accumulated in consumers of large biomass, resulting in conservation. Although there appears to be a framework for the examination of consumer regulation of both energy and nutrient cycling processes, few details of individual consumer impact have been quantitatively described. Given the complexity of functional regulation, there is little wonder that the effects of pollutants on regulatory interactions have not been properly investigated.

The simplest example of disruption of regulatory processes by pollution is the elimination of grazing species by increased mortality or by stress-induced emmigration. In aquatic systems, pollutant reduction of grazers is frequently followed by phytoplankton increases, often to bloom proportions (previously discussed in section 6.3). The control of primary production by grazers in aquatic systems is also diminished through pollution-induced composition changes in the producer community towards less preferable and less edible species. Large populations of mosses and filamentous algae are sometimes established in acidified lakes and streams, and the existing plant community becomes less diverse, thereby reducing the variety of species available to consumer levels, and hence, reducing the food supply (Hendrey *et al.*, 1976). The long-term input of a variety of pollutants into areas of the New York Bight has altered macrobenthic communities in the Christiaensen Basin (Boesch, 1979). Populations of species which are the predominant food for fish have been reduced. Therefore, although this basin supports a dense and productive benthic community, little of this productivity appears to be transferred up the food web.

Changed predator–prey relations in acidified lakes may be responsible for many of the biological changes reported (Eriksson *et al.*, 1980; Henrikson *et al.*, 1980). In acid lakes where fish populations have disappeared, they have been replaced by invertebrate top predators with different feeding strategies. Invertebrate zooplankton feeders, unlike fish, generally take smaller prey, which results in the proliferation of the larger species. The new grazer community of predominantly large species may, in turn, have an impact on phytoplankton productivity through changes in grazing pressure.

There is some evidence that simplification has potentially greater impact on the upper links in the food chain. Several investigators have suggested that there are significant differences in dietary strategy, in polluted versus unpolluted ecosystems, which reflect either changes in consumer behaviour or prey abundance, or perhaps both (Södergren, 1976; Jeffree and Williams, 1980). Predators may be eliminated for lack of quantity and quality of prey, as well as through direct toxic mortality (Pimentel, 1971). Hurlbert (1971) found that an organophosphorous insecticide had a more severe impact on primarily predaceous insects than on primarily grazing or collecting species. This was also noted by Stickel (1975) for other toxic compounds. Södergren (1976) attributed the decline in a salmon population to reduced prey abundance in metal-and acid-polluted waters.

Consumer–consumer interactions amended by pollutant introduction are exemplified by species population explosions upon elimination of natural predators due to pesticides (reviewed by Pimentel, 1972). In addition, Nounou (1980) showed that oil induced a series of relatively rapid oscillations in some consumer populations through elimination of certain species.

Pollution-induced perturbations have been observed to be passed up the food chain. Saward *et al.* (1975), in a microcosm study, showed that sublethal concentrations of copper (10, 30 and 100 μg l^{-1}) reduced algal productivity, which reduced the growth of grazing snails and, in turn, reduced the available food and the growth of young snail-feeding fish. Certainly, the simplicity of the microcosm community did not allow for prey-switching behaviour to supplement consumer diets, but studies of this type do indicate the functional importance of specialized feeding relationships. Holdgate (1979) discussed the SO_2-induced elimination of lichens with a parallel decline in a lichen-specific feeding insect (Psocidae) as exemplifying this type of trophic repercussion.

As an indirect result of normal consumer activity, toxic materials are accumulated and transported within polluted ecosystems. Most toxic pollutants are accumulated in biota at higher than ambient levels (Hutchinson *et al.*, 1975). There is evidence that some pollutants (organic pesticides and certain metals) are progressively accumulated up through the food chain. Trophic accumulation has been demonstrated for DDT in flesh-eating birds such as ospreys, peregrine falcons, Cooper's hawks, pelicans and a number of others (Ratcliffe, 1973; Snyder *et al.*, 1973; Stickel, 1973). Methylmercury is a pollutant which is bioaccumulated through food (Armstrong and Hamilton, 1973) and has caused human sickness and death; the Minamata incident is the most notorious example, with respect to man, of trophic accumulation and consequent toxicity. (See NRCC, 1979, for a review of mercury bioaccumulation and toxicity.)

6.5 ASSESSING CHANGES IN ENERGY FLOW AND NUTRIENT CYCLING

Changes in the characteristics of ecosystem function listed in Figure 6.1, and discussed in the previous sections, can provide quantitative data on ecosystem-level response to pollutant perturbations. However, the analysis of functional processes in pollution studies has had a relatively short history and is dependent upon the development of ecosystem theory and the collection of sufficient baseline data to establish 'normal' process rates.

With the development of ecosystem theory and methodologies, a number of more sophisticated functional indices have been proposed for pollution evaluation (O'Neill *et al.*, 1981). Power, defined as the total energy movement through the ecosystem per unit biomass, is a metabolic index which should respond to perturbation and which is related to the maximization of persistent biomass. Odum and Pinkerton (1955) and Odum *et al.* (1977) have argued that through the interaction of low quality energy (solar radiation) and high quality energy (biomass), power influences the capability of the ecosystem to respond to perturbations. Power has been related to both the ability of the system to recover from disturbance (O'Neill, 1976) and the time between perturbation and recovery (DeAngelis, 1980).

The characteristic of phase space has been used to describe an ecosystem in terms of a matrix of redox reactions (Schindler *et al.*, 1980b). The phase-space response (pH–dissolved oxygen) of an aquatic microcosm has been demonstrated for physical (stirring), chemical (acidification) and biological (species introduction) perturbations (Waide *et al.*, 1980).

The analysis of frequencies of response has been used to characterize periodicities in metabolism, biomass and nutrient stability (Emanuel *et al.*, 1978a, b; Van Voris *et al.*, 1980). The number of low-frequency peaks in CO_2 efflux was suggested as an index of functional complexity of the ecosystem, with the assumption that the periodicity of peaks must be related to functional interactions among components, as influenced by feedbacks and time delays. Recently, Dwyer and Perez (1983) reported that the number of functional periodicities was reduced when the complexity of the microcosm community was simplified.

A cycling index quantifying energy and material flows has been suggested by Finn (1976, 1980). The path length (*PL*) is defined as the number of compartments through which the inflow passes, and the cycling index (*CI*) is the proportion of flow that cycles through components of the system. Flow indices can characterize the nutrient cycling in different ecosystems, however, the relationship of *CI* to other measures of cycling (leachability and turnover rate) is presently unclear (Finn, 1980). Although these indices offer an elegant mechanism for representing the complex processes of cycling through a single numeric quantity, their value in assessing the impact of disturbances to ecosystems has not yet been demonstrated (May, 1981).

In streams where nutrient retention processes are competing with downstream transport, recycling has been described in terms of the concept of spiralling length (Wallace *et al.*, 1977; Webster and Patten, 1979). Spiralling can be visualized as the number of times particulate organic matter is taken up by feeding organisms as it is transported downstream, i.e. the shorter the distance between reingestions, the tighter the spiral. Using radiotracers, spiralling length can be measured in natural ecosystems (Newbold *et al.*, 1981), although the effects of pollutants on this process have not yet been evaluated.

The ecosystem is the fundamental unit in ecology and must be recognized as such in ecotoxicology. There is a theoretical base and a developing research methodology for the analysis of changes in energy and cycling processes in perturbed ecosystems. The complexities of natural systems should not dissuade scientists from focusing their efforts on understanding the effects of toxic pollutants on the state of the whole ecosystem.