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EFFECTS OF SULPHUR DIOXIDE POLLUTION ON LITTER DECOMPOSITION IN A COOL TEMPERATE PINE FOREST

by

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "EFFECTS OF SULPHUR DIOXIDE POLLUTION ON LITTER DECOMPOSITION IN A COOL TEMPERATE PINE FOREST," submitted by CINDY ELLEN PRESCOTT in partial fulfillment of the requirements for the degree of Master of Science.

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ABSTRACT

Litter decomposition was measured at 3 "ecologically analogous" pine (P. contorta x P. banksiana) stands located (1) 2.8 km, (2) 6.0 km and (3) 9.6 km from a sour gas plant which had been emitting low levels of SO_2 for 20 years. Respiration of intact forest floor cores, and separated litter, fermentation, humus and mineral soil layers was consistently lowest at site 1 and highest at site 3. Rates of mass loss and respiration of pine needles decomposed in litterbags for 17 months also increased with distance from the gas plant. Decomposition of needles in exchanged litterbags was related primarily to site of origin during the first few months of decomposition, and to site of placement thereafter. Litterfall rates did not bear any relation to sulphur loading, however, litter accumulation and residence times were greatest at the site nearest the gas plant. These findings indicate that an inhibition of decomposition activity has occurred in response to elevated levels of SO_2 pollution. The long-term suppression of decomposition activity hence nutrient release may be contributing to the lower rates of primary productivity at sites near the gas plant. The use of decomposition measurements and ecologically analogous sites is recommended for ecological monitoring studies.

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INTRODUCTION

Sulphur Dioxide Pollution

The disruption of natural ecosystems as a result of human activities is an increasingly common occurence throughout the world. Identification and understanding of such impacts is essential if effective decisions are to be made, leading to reductions in the severity of the disruptions. The combustion of fossil fuels for energy production is an extremely widespread activity which may lead to environmental degradation. The extensive impacts resulting from fuel combustion are largely the result of the oxidation of sulphur compounds contained in the fuel, with the subsequent release of sulphur oxides to the environment.

The Global Sulphur Cycle

Sulphur occurs naturally in a number of forms: elemental sulphur, sulphide, sulphate, sulphur dioxide, sulphuric acid, hydrogen sulphide and organic sulphur, which change as the element is transported among its reservoirs (Moss 1978). Several attempts to quantify these fluxes and reservoirs have been made, with variable results.

A major reservoir for sulphur is the atmosphere, where it is present as SO_2, $SO_4^{=}$ and H_2S. The largest source of atmospheric sulphur is from biological decay, which releases

H_2S. The H_2S is oxidized to SO_2 via a number of reactions. Anthropogenic emissions represent the second largest flux of sulphur to the atmosphere. Atmospheric SO_2 may be oxidized to $SO_4^{=}$, which may also arise from windblown salts. Volcanoes emit relatively small amounts of each of these compounds.

Sulphur returns to the earth's surface primarily as SO_2 and $SO_4^{=}$ in precipitation with smaller amounts absorbed as gaseous SO_2 or deposited as sulphate particles. SO_2 absorbed by vegetation, soil or water surfaces is rapidly oxidized to sulphate. Vegetation also takes in sulphur from soil, and returns it mostly in organic form upon death. Organic sulphur is converted by soil microbes directly to $SO_4^{=}$ or to H_2S , which is released to the atmosphere or converted to sulphate or to elemental sulphur and then $SO_4^{=}$. The sulphates may be reduced to sulphides and volatilized, immobilized by plants or microbes, insolubilized by cations, or lost in drainage water. Sulphate in water bodies is eventually returned to earth in sea salt or deposited in sediments. Rock weathering also contributes some sulphate to soil and water.

Anthropogenic Sulphur Emissions

Man-made emissions of sulphur to the atmosphere have been estimated at 40 - 65 million tonnes per year (Moss 1978). About 95% of these emissions are in the form of SO_2, the remainder is composed of H_2S, SF_6 and mercaptans

(Kellogg et al. 1972). On a global scale, fossil fuel combustion contributes approximately 85% of total man-made sulphur emissions, with ore-smelting and petroleum refining accounting for an additional 11% and 4%, respectively (Brown 1982). Global distribution of sulphur emission sources is very uneven, as 94% is produced in the northern hemisphere (Kellogg et al. 1972). Anthropogenic emissions are thought to account for slightly more than half of total sulphur emissions (Granat et al. 1976). However, in industrial regions such as western and central Europe and eastern North America, anthropogenic emissions account for more than 90% of total sulphur emissions (National Research Council of Canada 1981). About 33% of world emissions arise in western and central Europe, while North America contributes about 25% (National Research Council of Canada 1981). In 1980, this amounted to 28.8 million tonnes of SO_2 from the U.S. and 4.8 million tonnes from Canada (Ontario Ministry of the Environment 1981). In the U.S., 55% of the sulphur emissions are produced by power-generating plants, while in Canada, 43% is produced by non-ferrous smelting operations, 22% by other industries, and 14% by power plants (Ontario Ministry of the Environment 1981). 71 per cent of U.S. emissions originate east of the Mississippi, while 83% of Canadian sulphur emissions originate

east of Saskatchewan (Ontario Ministry of the Environment 1981).

Atmospheric Transformation of Sulphur Dioxide

Sulphur dioxide released to the atmosphere is converted to sulphates and sulphuric acid aerosols via a number of complex chemical reactions. Homogeneous reactions occur through direct photo-oxidation upon gas-phase collisions with strong oxidizing radicals (U.S. Department of Energy 1980). The sulphate and sulphuric acid aerosols formed are rapidly taken up by water vapour and incorporated into droplets (Fowler 1980). Heterogeneous reactions involve the oxidation of gaseous SO_2 absorbed to particles or in droplets (Tanner et al.1981). Heterogeneous oxidation reactions are believed to account for about 90% of the SO_2 removed (Friend 1980 as cited in U.S. Department of Energy 1980). Rates of both reactions vary according to atmospheric conditions (Sandhu et al. 1980, U.S. Department of Energy 1980) and are not generally agreed upon (Dovland and Semb 1980). Sulphur dioxide dissolved in droplets rapidly reaches an equilibrium between dissolved SO_2, H_2SO_3, HSO_3^- and $SO_3^=$ in a few seconds (Gravenhorst et al. 1980). The relative amounts of each anion at equilibrium depend on the pH of the solution. Upon oxidation these products are transformed to sulphuric acid aerosols which

may react with metal oxides in dust to form salts such as ammonium sulphate and calcium sulphate (Moss 1978).

Deposition of Atmospheric Sulphur Compounds

Sulphur dioxide and its oxidation products return to the earth's surface through both wet and dry deposition. Dry deposition involves direct absorption of gaseous SO_2 or settling out of particulate sulphates onto soil, vegetation or water surfaces (Fowler 1980). Gaseous absorption accounts for the bulk of dry deposited sulphur (Fowler 1980). Dry deposition of sulphur shows a clear relationship to emission source, and is generally the major form of deposition in polluted areas (Moss 1978). Wet deposition involves the diffusion of gases or particles into water droplets while in clouds (rainout) or during descent of raindrops (washout) (Fowler 1980). Rainout generally accounts for most of the sulphur in rain (Fowler 1980). Over 90% of sulphur in precipitation is usually in the form of sulphate, although dissolved SO_2 may contribute up to 25% of total sulphur in winter (Dovland and Semb 1980). Wet deposition of sulphate shows maxima in source areas and also in non-source areas receiving precipitation from air masses transported from areas of high emissions (Moss 1978). Depending on prevailing climatic conditions, this form of deposition tends to become increasingly important with distance from the source (Fowler 1980).

This relationship is evident in regional estimates of dry to wet deposition ratios (Galloway and Whelpdale 1980): eastern Canada - 0.4, Norway - 0.3, eastern U.S. - 1.2, U.K. - 3.0. In addition, the interception of precipitation by vegetation, and the resultant washoff of deposited compounds may lead to elevated sulphate levels in throughfall in polluted areas (Lindberg and Harriss 1981, Mayer and Ulrich 1980).

Acid Precipitation

Most of the sulphate deposited in precipitation has been neutralized by atmospheric ammonia or other basic particles (Urone and Schroeder 1978). However, in areas where the sulphur concentrations exceed equivalent amounts of ammonia, much of the acid will not be neutralized prior to deposition and precipitation will become more acidic. The oxidation of atmospheric nitrous oxides to nitric acid is a lesser but significant source of precipitation acidity in most areas. Acid precipitation has become common in areas of the world producing large amounts of SO_2 and NO_x pollution, and also in areas receiving these polluted air masses, since transformation to acid occurs during transport. The average acidity of precipitation in the northeastern U.S., eastern Canada and Scandinavia is pH 4, and individual events as low as pH 2.1 have been recorded (Likens and Bormann 1974, National Research Council of Canada 1981). The dramatic

increase in precipitation acidity in the last two decades is believed to be the result of pollution control measures such as use of cleaner fuels and higher stacks and the removal of particulates which allow the gases to be transported farther and more completely converted to acid (Likens and Bormann 1974). Although "acid rain" has received the most attention, it is recognized that dry-deposited sulphur compunds are also capable of acidifying the environment in which they land, as they are rapidly hydrolyzed on soil, water or vegetation surfaces. Thus, deposition of "acidifying substances" in both wet and dry forms is of concern (Grennfelt et al. 1980, Kerr 1981).

Sulphur Extraction Gas Plants

The major sources of sulphur dioxide in the province of Alberta are sulphur extraction gas plants. Basically, this industry removes hydrogen sulphide from "sour" natural gas, thereby converting it to saleable "sweet" gas. Most of the H_2S removed is converted to elemental sulphur which is shipped in liquid or pellet forms to market or stockpiled near the plant. The average efficiency of this conversion in sulphur extraction gas plants is 97% (Energy Resources Conservation Board 1982). The unreacted H_2S is incinerated at 500^{o}C and released through a stack to the atmosphere as SO_2 (Sandhu et al. 1980).

There are 109 sour gas processing plants in operation in Alberta; 45 of these have sulphur recovery processes while the remainder are of smaller capacity and simply flare the gas (Energy Resources Conservation Board 1982). The natural gas industry in Alberta has grown rapidly in the last 20 years (Energy Resources Conservation Board 1982). In 1981, Alberta produced 62 billion cubic meters of marketable gas (88% of Canadian production) and 5.6 million tonnes of sulphur (Alberta Economic Development 1982). Sulphur emissions from this industry amount to about 140,000 tonnes per year, which equals 60% of Alberta emissions and 13% of total Canadian sulphur emissions (Hammer 1980).

The fate of the SO_2 emitted from gas plants is not well understood (Sandhu et al. 1980). The average atmospheric lifetime of SO_2 in Alberta is 3.5 days in summer and 522 days in winter (Sandhu et al. 1980). In winter, very little sulphur is deposited near the source, since absorption by snow is very inefficient (Fisher 1978). Nyborg et al. (1977) determined the sulphur content and pH of snowpack downwind of a large SO_2 source to be similar to that found in areas remote from pollution sources (0.5 kg S ha^{-1}, pH 5-6). Rainfall is much more efficient at removing SO_2. Nyborg et al. (1977) reported the sulphur content of rain in Alberta to be about 5 times that of snow, contributing 4 kg S ha^{-1} near SO_2 sources as compared with about 1 kg S ha^{-1} $year^{-1}$

in remote areas. Summers and Hitchon (1973) found that 32-46% of the SO_2 emitted by a gas plant was deposited within 25 km by summer convective storms, compared with 2% deposited in snowfall. This situation is believed to be peculiar to gas plants located near the Rocky Mountain foothills. The pH of rain in Alberta is seldom acidic as most acid is neutralized by salts (Nyborg et al. 1977). However, rain intercepted by trees exposed to SO_2 emissions has been found to have pH levels of 3.5 - 4.5 and sulphur contents 3-4 times higher than that of incident rainfall (Baker et al. 1977, Nyborg et al. 1977).

Dry deposition appears to be more important in removing SO_2 emitted from gas plants from the atmosphere in Alberta, probably due to the relatively arid climate. Caiazza et al. (1978) determined the mean ratio of dry deposited to wet deposited sulphur in central Alberta to be 4.8. Deposition of SO_2 through absorption was reported as being 10 times that deposited in rainfall (Nyborg et al. 1977). Soils absorb large amounts of SO_2 from emissions (4-20 kg SO_4 ha^{-1} within 11 km of a gas plant - Nyborg et al. 1977).

Although much of the SO_2 emitted from gas plants may be transported long distances (especially in winter), large amounts tend to be deposited near the source. Walker et al. (1981) reported sulphur absorption by soil, water and rainfall all 2-3 times higher within an area of high sulphur

emissions as compared with more distant sites (more than 40 km away).

A second type of sulphur pollution from gas plants is elemental sulphur dust which is liberated during disturbance of storage blocks. The dust may be carried by wind, but is mostly deposited within 2-4 km of the plant, at concentrations ranging from 1 to 100 tonnes ha^{-1} (Nyborg 1978).

Environmental Effects of SO_2 Pollution

The ecological impacts of SO_2 pollution are primarily related to the acidification potential of its oxidation products. Very dramatic effects of acidification of aquatic ecosystems, including altered chemical composition and reductions in abundance and diversity at all trophic levels, have been reported (Almer et al. 1974, Beamish 1974, Hendrey et al. 1976, Wright and Gjessing 1976). Exposure of terrestrial vegetation to acidifying substances has been found to cause structural damage, nutrient leaching, premature senescence and abcission, altered nutrient status, disruption of photosynthesis, respiration and gas-exchange processes, increased sensitivity to stress, and reduced rates of growth and seedling development (Knabe 1976, Linzon 1978, Malhotra and Hocking 1976, Smith 1981, Tamm and Cowling 1976, Wood and Boormann 1977). Depending on the degree of pollution and the relative sensitivities of the plants, reduced diversity

and altered species composition of plant communities may result (Freedman and Hutchinson 1980a, Gorham and Gordon 1963). Many of these alterations in vegetational characteristics have been reported near gas plants (Hocking 1975, Legge et al. 1978, Legge and Bogner 1982, Nyborg 1978, Winner and Bewley 1982).

Sulphur dioxide, elemental sulphur and ammonium sulphate are all capable of acidifying soil as all may be converted to H_2SO_4 (Nyborg 1978). Sulphates formed from the dissociation of H_2SO_4 in water combine with metallic cations (especially calcium) in soil solution to form metallic sulphates which tend to be leached from the soil. Depending on the degree of acid input and the concentrations of exchangeable cations present in the soil, reduced base saturation and pH levels may result. This may create deficiencies of the basic cations for plants and microorganisms. In addition, the lower pH may lead to higher levels of some metals (especially aluminum, manganese and iron) which may, in conjunction with the acidity, result in conditions toxic to many organisms (Nyborg 1978). Each of these chemical changes have been detected in soils near gas plants (Baker et al. 1977). Along with the direct effects of exposure on vegetation, alterations of soil properties and nutrient availabilities, have been proposed to lead to alterations in nutrient cycling processes, hence

reductions in forest growth (Johnson et al. 1981, Jonsson 1977, Tamm 1976).

Nutrient Cycling

In addition to global biogeochemical cycles such as the sulphur cycle, there exist within ecosystems transfers of essential elements between the various biotic and abiotic components of the system (Odum 1971). In terrestrial ecosystems, a portion of the nutrient supply is gained from the atmosphere and from rock weathering, and some is lost through leaching and volatilization. However, most of the nutrient supply is continually transferred among components and thereby retained within the system. Nutrients taken up from the soil solution are converted into biomass by vegetation; this organic matter may be consumed by herbivores and returned to the soil as excreta or upon death, or returned directly as litter. During decomposition, these organic materials are broken down and the contained nutrients are released in simpler forms suitable for uptake by primary producers.

Litter Decomposition

As the dominant process by which nutrients become available to plants, the decomposition of organic matter is an essential factor in the maintenance of internal element cycles, hence productivity of ecosystems. An estimated 80 to 90%

of net primary production in terrestrial ecosystems is eventually converted and recycled by these decomposer organisms (Odum 1971). Decomposition is primarily a biological process performed through the enzymatic activities of microbes (bacteria and fungi) and comminutive activities of soil invertebrates. Mechanical weathering of litter, and chemical leaching of its soluble constituents are also involved in the decomposition process (Anderson 1973).

A number of methods may be used to measure rates of decomposition (Parkinson et al. 1971, Singh and Gupta 1977, Smith 1981, Swift et al. 1979). However, due to the complexity of the process, no completely accurate and reliable method of measurement has been developed. Instead, the measurement of a number of related parameters is recommended (Ausmus 1973, Woods and Raison 1982). Loss of dry mass of litter or other substrates in mesh bags or other enclosures in the field is a direct method for estimating decomposition rates (Witkamp and Olson 1963). Respiration (O_2 or CO_2 flux) of soil or litter with or without amendments provides an estimate of heterotrophic activity, hence decomposition rates (Minderman and Vulto, 1973, Witkamp 1966). The ratio of litterfall to litter standing crop can be used as an estimate of litter turnover rates (Olson 1963). Estimates of numbers or mass of decomposer organisms will also provide an estimate of potential decomposition activity (Parkinson et al. 1971).

Effects of Sulphur Pollution on Litter Decomposition

Due to the importance of litter decomposition in the cycling of nutrients within ecosystems, a disruption of this process could have detrimental repercussions on primary production and ecosystem stability. Reduced rates of forest litter decomposition resulting from acidification by sulphur pollution have been postulated by a number of authors (Malmer 1976, Oden 1968, Tamm et al. 1977), and have been proposed as factors linking sulphur pollution to reduced forest productivity (Tamm 1976). It is well known that organisms responsible for decomposition are sensitive to acidity levels in their environment, and that decomposition usually proceeds more rapidly under neutral rather than acidic conditions (Alexander 1977, Nyborg 1978). Many decomposer organisms (especially bacteria) are inactive or less active when the pH of their environment drops below 5 (Williams and Gray 1974). This effect may be due to the hydrogen ion concentration itself (through interference with enzyme and membrane function), or to the resultant alterations in concentrations of other elements to toxic or insufficient levels. Gaseous SO_2 itself is probably not toxic to microorganisms, however, the bisulphite formed from the dissolution of SO_2 in water (rain, soil or cell surfaces) may be toxic to decomposer organisms (Babich and Stotzky 1982). Sulphite is less toxic than bisulphite (Babich and Stotzky 1982).

A number of laboratory investigations have revealed alterations in decomposition rates following the application of sulphuric acid or simulated acid rain to soil samples. Although results have varied, these short-term experiments have usually demonstrated reduced rates of decomposition at rain or soil pH levels below 3.5, and unaltered or stimulated decomposition at higher pH levels. Tamm and co-workers (1977) reported reduced rates of respiration over 8 weeks in humus samples from a pine forest pretreated with sulphuric acid. Application of pH 3.5 simulated rain for 5 or 25 weeks inhibited carbon mineralization in two forest soils of pH 4.1 and 3.9, but enhanced it in a more acid soil of pH 3.1 (Chang and Alexander 1981). Continuous or intermittent exposure of forest soil samples (pH 4.4 - 7.1) to simulated rain of pH 3.2 for 7 weeks led to depressed rates of glucose mineralization. Rain of pH 4.1 had no effect (Strayer and Alexander 1981). Similar application of acid rain for 19 weeks led to reduced rates of nitrification at both pH levels, but no change in nitrogen mineralization (Strayer et al. 1981). Similarly, Killham et al. (1973) found treatment with pH 2.0 simulated rain for 12 weeks to inhibit respiration and enzyme activity in a forest soil of pH 6.4. Application of rain of higher pH (3.0 and 4.0) stimulated these activities relative to controls treated with pH 5.6 rain. Kelly and Edwards (1983) found no differences in respiration of intact

forest floor microcosms following application of simulated acid rain of pH 3.5 - 5.7. However, respiration of separated F and H material was consistently greatest in the pH 4.0 treatment microcosm, and least in the pH 3.5 microcosm.

The acidification of oak-pine forest soil from pH 4.6 to 3.0 with sulphuric acid resulted in reduced rates of respiration, ammonification, denitrification and nitrification after pre-incubation for 14 or 150 days. Increases in these parameters were observed when pH levels were elevated to 7.0 with calcium hydroxide (Francis 1982). Similarly, Bewley and Stotzky (1983) found acidification of soil samples of pH 4.8 with sulphuric acid to lead to diminished rates of glucose degradation at pH 3.0, and complete inhibition of this process at pH 2.0. Glucose mineralization was restored when the pH of the soil was raised to 4.1. Growth of several species of fungi were reduced or eliminated in soils acidified below pH 3.5.

Field experiments involving the application of simulated acid rain to forest soils _in situ_ have also demonstrated contrasting results as to the effects of acidity on decomposition rates or on populations or activities of decomposer organisms. Roberts and co-workers (1980) reported increased rates of mass loss of _Pinus nigra_ litter, but unaltered respiration of organic layers following treatment of forest plots with pH 2.7 and 3.1 sulphuric acid for 5 months.

Lodgepole pine needles which had been exposed to pH 3.0 "rain" for 1 year demonstrated elevated rates of mass loss during a 90 day incubation period, relative to control needles treated with pH 5.6 rain (Ishac and Hovland 1976). Incubation of control needles in dilute sulphuric acid for 105 days led to reduced and negligible mass loss at pH 1.8 and 1.0, respectively. No change in mass loss rates were observed in needles incubated at pH levels of 3.5 and above.

In a similar experiment in a Norway spruce forest treated for 5 years with acidified rain, Hovland (1981) reported lower cellulase activity, but unaltered respiration rates at litter pH levels of 3.5 and 4.0. Treatment of control needles with acidified rain for 38 weeks resulted in slight reductions in mass loss and lignin decomposition rates at pH 3.0 and 2.0, and diminished respiration at pH 2.0 (Hovland et al. 1980). Hagvar and Kjondal (1981) found mass loss of birch leaves in litterbags incubated for 3 years in a forest or 3 months in a greenhouse to be inhibited by pH 2.0, but not pH 3.0 or 4.0 sulphuric acid. Decomposition of hardwood leaf litter packs was stimulated by the addition of simulated acid rain of pH 3.5 to forest plots, as compared with control plots receiving pH 5.6 "rain" (Lee and Weber 1983).

In a Scots pine forest watered with acidified rain for 5 years, Baath and co-workers (1979) observed lower respiration rates, FDA-active bacteria and fungal lengths and bacterial

cell size, but no change in total fungal length or bacterial numbers at lower pH levels (3.4 and 2.5). In a more extensive investigation (Baath et al. 1980) in another Scots pine forest treated with acidified rain for 6 years, reduced FDA-active fungal lengths and bacterial cell size and number were observed on acidified plots. Alterations in populations of soil and litter fauna have also been observed in forest plots exposed to artificial acid rain. The most common modifications were reduced populations of most species, especially enchytraeids and mites, and increased abundance of some species of collembolans (Baath et al. 1980, Hagvar and Abrahamsen 1977, 1980, Hagvar and Admundsen 1981, Hagvar and Kjondal 1981), although results have been variable.

Treatment of soils with other forms of sulphur (SO_2, sulphite, bisulphite or elemental sulphur) have also revealed altered rates of decomposition. Lower rates of mass loss of western wheatgrass occurred when litter fumigated with low levels (200 ug m^{-3}) of SO_2 for 3 years was incubated for 5 months at the fumigated site, as compared with non-fumigated litter incubated at the control site which had received less than 26 ug m^{-3} (Dodd and Lauenroth 1981). Fumigated litter incubated at the control site exhibited mass loss rates intermediate but more similar to that of the controls, suggesting that the pH or sulphur content of the environment is more important than that of the substrate

in inhibiting decomposition. Reduced tardigrade densities but no significant changes in rotifer and nematode populations were found following these low-level SO_2 fumigations (Leetham et al. 1982). Reduced decomposition, but unaltered respiration rates were found in western wheatgrass exposed to 220 ug m^{-3} SO_2 under laboratory conditions (Leetham et al. 1983).

Respiration of Pinus nigra litter was reduced following exposure to SO_2 (650 ug m^{-3}) for 35 days (Ineson and Gray 1980). Acidification of this litter in the absence of SO_2 did not lead to any inhibition of decomposition (Ineson and Roberts 1981). Labeda and Alexander (1978) observed a reduction in nitrification rates following continuous exposure to 10 ppm (10,000 ug m^{-3}) SO_2 for 2 weeks in a soil sample of pH 5.0, but not in one of pH 7.2. Continuous or intermittent exposure to lower SO_2 levels had no effect.

Exposure of a forest soil of pH 4.06 to 1.0 ppm (1000 ug m^{-3}) SO_2 for 12 days resulted in diminished rates of glucose degradation (Grant et al. 1979). The addition of 5 ug bisulphite per gram of soil did not affect glucose decomposition rates, however bisulphite in combination with nitrite was more inhibitory than nitrite alone, suggesting a synergistic relationship. Grant et al. (1980) reported delayed amino acid degradation in soil treated with 1 or 5 ppm (1000 or 5000 ug m^{-3}) SO_2 for 24 or 48 hours, respectively. Comparable levels of bisulphite were less effective, but

became more inhibitory when the pH was reduced slightly to 3.89. Comparable levels of sulphate did not inhibit carbon mineralization. Babich and Stotzky (1978) found that growth of bacteria and fungi was more sensitive to high levels of bisulphite than sulphite, and the toxicity of both anions increased with increasing acidity of soil. Bryant et al. (1979) found considerably lower bacterial numbers and decomposition rates of starch, cellulose, urea, glucose and casein in soil of pH 3.0 one meter from a sulphur storage block, as compared with that 200 m away (pH 6.8).

Most field studies utilizing existing pollution sources have examined effects of sulphur in combination with other pollutants. Wainwright (1980) could not detect any changes in microbial numbers, respiration or nitrification rates or enzyme activity in a woodland soil transferred from an unpolluted site to one receiving pollution (125 ug $SO_2 \cdot m^{-3}$) from a coking plant for 1 year, despite a reduction in pH from 4.2 to 3.7. Killham and Wainwright (1981) observed reduced rates of sycamore leaf litter decomposition and reductions in arthropod numbers and diversity after 6 months at a site receiving pollution from a coking plant, as compared with those at an unpolluted site. Exchanged litter showed intermediate mass loss, suggesting that both substrate and ambient pollution levels are important in inhibiting decomposition. Cellulose degradation was only marginally inhibited.

Freedman and Hutchinson (1980b) reported greater litter standing crop and lower rates of litter decomposition and respiration rates and acid phosphatase activity in the vicinity of a large nickel-copper smelter. However, the effects were believed to be primarily due to the heavy metals emitted in addition to the SO_2 and sulphuric acid mists.

Several investigations have indicated considerable inhibition of microbial decomposition in waters receiving acid precipitation (Hendrey and Barvenik 1978). Reduced bacterial activity and decomposition of leaves in litterbags, accumulation of coarse organic detritus, and abnormally thick fungal mats have all been observed in Swedish lakes which have undergone rapid acidification in recent years (Grahn et al. 1974, Hendrey et al. 1976). Traaen (1980) reported reduced biochemical oxygen demand during decomposition of glucose, glutamic acid and birch leaf litter in laboratory respirometers at pH 5.2 and 4.0 relative to pH 7.0 controls, and reduced rates of mass loss of birch leaves at pH levels below 5.0 after 1 year in flow through tanks or after 2 years in natural waters. The acidification of lake waters in microcosms from pH 7.4 to 3.0 or 4.0 resulted in reduced rates of mass loss, colonization, and lignocellulose degradation within 18 days (McKinley and Vestal 1982).

It is apparent from the existing literature that the addition of sulphur to litter or soil can alter decomposition

rates and populations and activities of decomposer organisms. However, these effects have not been consistent, and have usually been found in experiments using artificial conditions and unrealistically high concentrations of sulphur or mixtures of pollutants. In contrast, the present study examined effects of low-level, long-term sulphur pollution on a natural forest community. Effects of dry deposition of essentially pure SO_2 were examined, so that effects of this type of pollution could be determined and compared with those of acid precipitation.

The aim of the present research project was to compare rates of litter decomposition in three pine stands exposed to different levels of SO_2 pollution. More specific research objectives were: 1) to determine rates of respiration of soil and litter at each site, 2) to measure rates of mass loss of needles at each site over a 1.5 year period, and 3) to quantify litter input, accumulation and residence times at the 3 sites.

STUDY AREA AND SITE DESCRIPTION

The sites chosen for the study are located approximately 45 km west of Whitecourt, in west-central Alberta, Canada (54°15'N, 116°W). This is an area of transition between the boreal and subalpine forest regions (Legge et al. 1978). Major tree species present include lodgepole-jack pine (Pinus contorta Loud. X Pinus banksiana Lamb.), black spruce (Picea mariana Mill.) and balsam poplar (Populus balsamifera L.). Bear-berry (Arctostaphylos uva-ursi (L.) Spreng.) is the major understory vegetation at each of the sites (Legge et al. 1978). The area has a rolling topography of dunes and bogs, and soil described as degraded eutric brunisol. The climate is subhumid continental with large seasonal and diurnal temperature fluctuations. Mean monthly temperatures in 1982 ranged from -25.5°C in January to 15.5°C in July, with an annual average of 0.3°C. 1983 mean monthly temperatures ranged from -18.8°C in December to 16.2°C in August, with an annual average of 1.3°C (Figures 1 and 2). Total annual precipitation was 594.1 mm in 1982 and 571.2 mm in 1983. Snow cover is continuous from November through March.

The source of sulphur dioxide in the area is the AMOCO Canada Petroleum Co. Ltd. West Whitecourt (Windfall) gas processing plant. This plant currently emits about 36 tonnes of SO_2 per day, but has released considerably larger amounts

Figure 1. Daily climatic data for the Whitecourt area for the period 1 January 1982 - 31 December 1982.

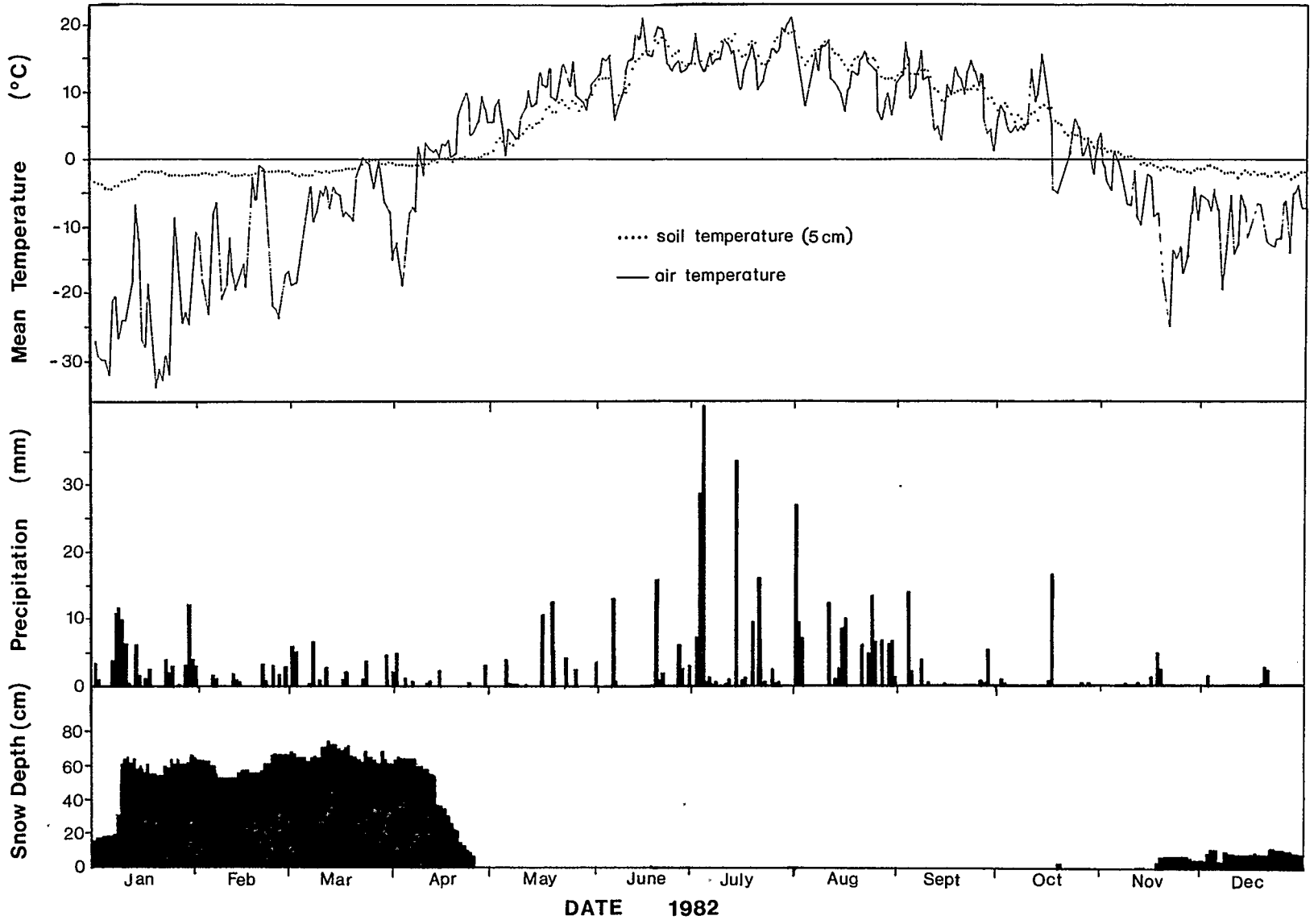
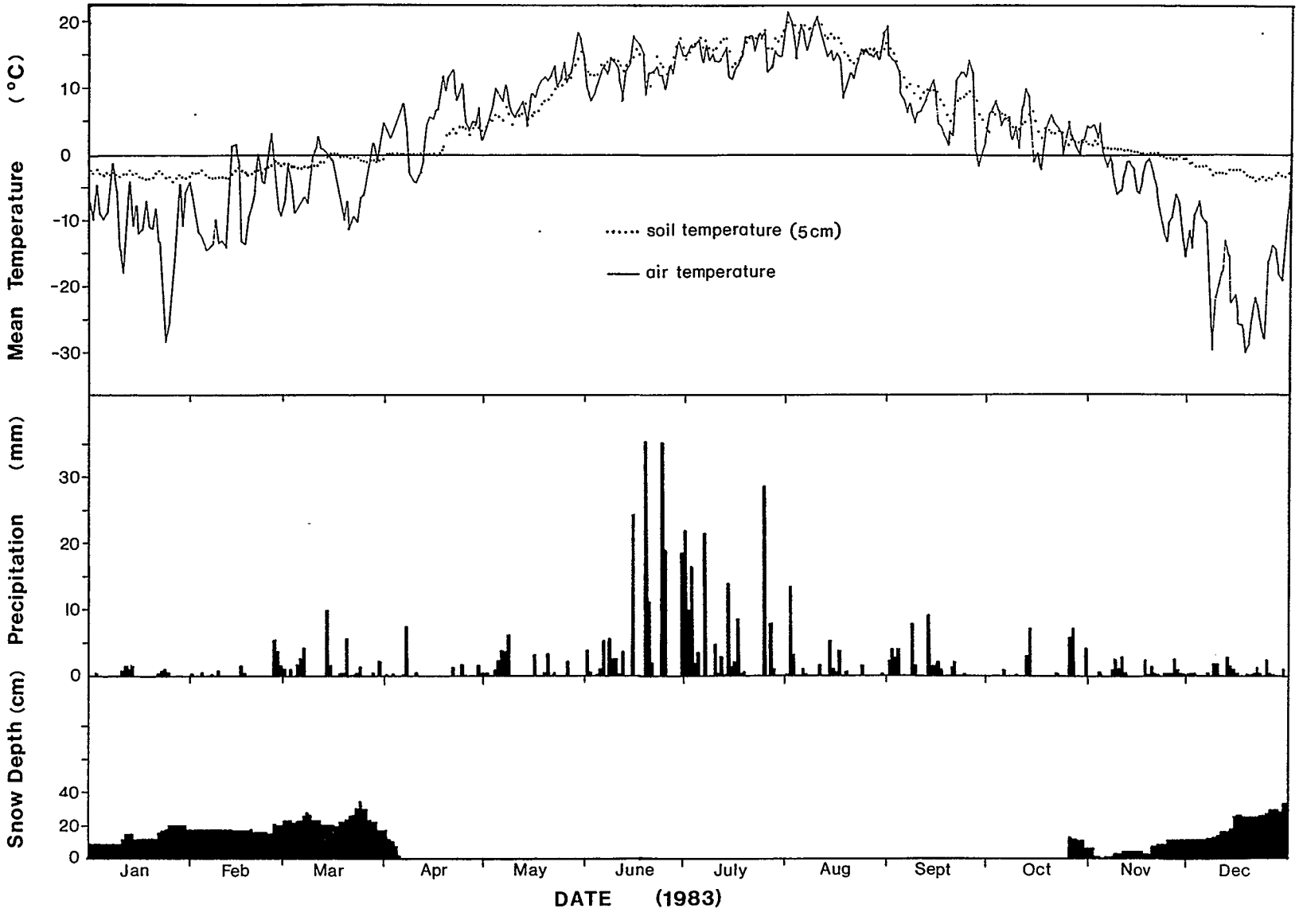

Mean Temperature (°C)
20
10
0
-10
-20
-30
..... soil temperature (5 cm)
—— air temperature
Precipitation (mm)
30
20
10
0
Snow Depth (cm)
80
60
40
20
0
Jan
Feb
Mar
Apr
May
June
July
Aug
Sept
Oct
Nov
Dec
DATE 1982

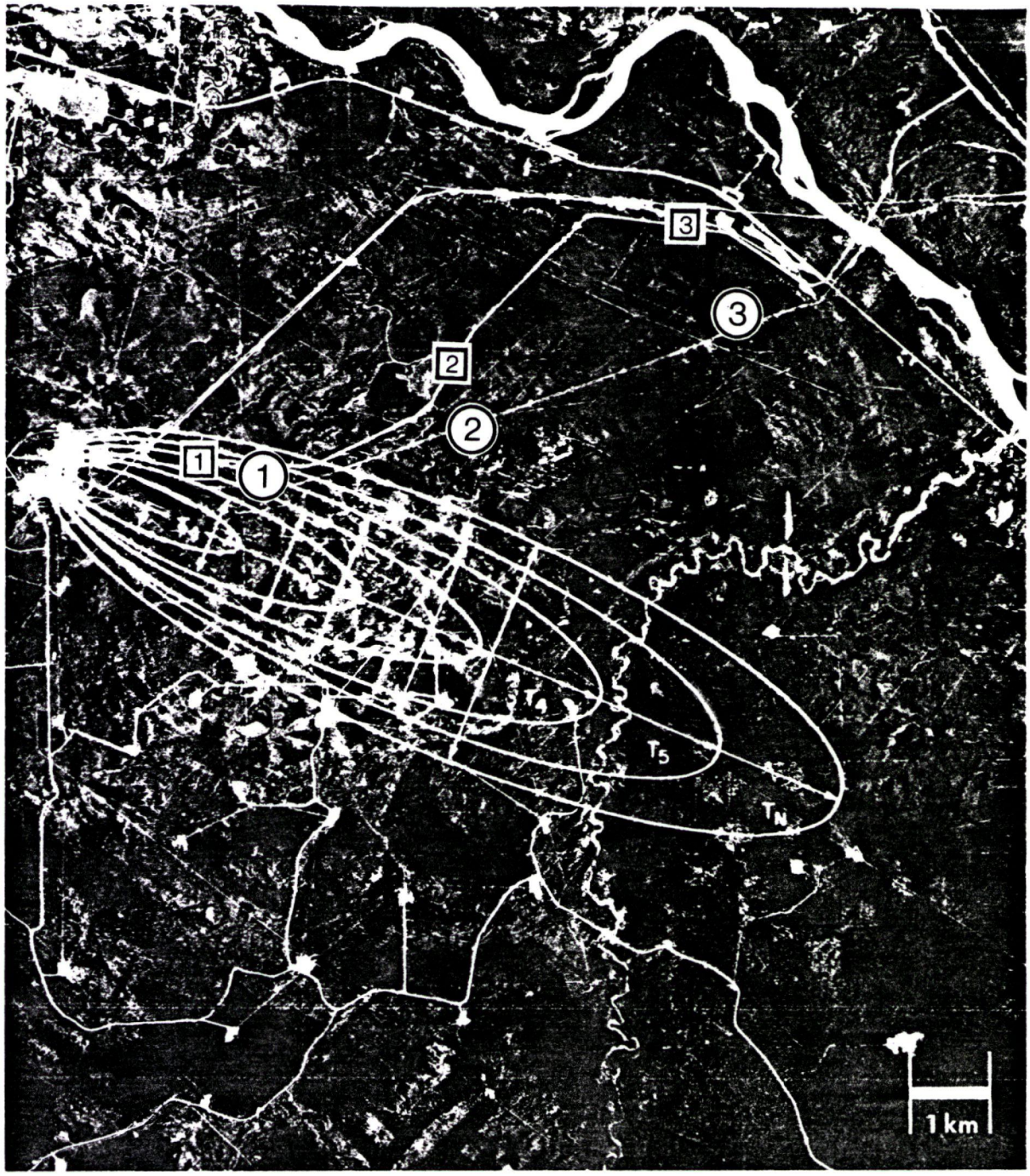
Figure 2. Daily climatic data for the Whitecourt area for the period 1 January 1983 - 31 December 1983.


Mean Temperature (°C)
20
10
0
-10
-20
-30
..... soil temperature (5cm)
—— air temperature
Precipitation (mm)
30
20
10
0
Snow Depth (cm)
40
20
0
Jan
Feb
Mar
Apr
May
June
July
Aug
Sept
Oct
Nov
Dec
DATE (1983)

in past years (300 tonnes per day at its initiation in 1962) (Legge et al. 1978; Legge and Bogner 1982). The plume from the Windfall plant usually follows a WNW to ESE corridor (Legge et al. 1977). For the purposes of this investigation, 3 sites were selected at increasing distances (2.8, 6.0 and 9.6 km) from the gas plant, and also from the main plume corridor (Figure 3). As a result, considerably smaller pollution loadings occur at the sites located farthest from the plant as compared with the one nearby (Legge et al. 1978). Total sulphation measurements (mg SO_3 100 cm^{-3} day^{-1}) in 1982 averaged 2.30, 2.00 and 0.92 near sites 1, 2 and 3, respectively (A. Legge, personal communication). Sites 1, 2 and 3 correspond to Analogues II, III and V of Legge et al. (1978).

The sites are situated on dunes occupied by pure stands of hybrid pine (P. contorta X P. banksiana). Extensive vegetational analysis by Legge and co-workers (1978) have determined the sites to be very similar in physiographic and vegetative characteristics (i.e. "ecologically analogous"). Soil pH at sites 1, 2 and 3 averaged 3.5, 4.7 and 4.8, respectively for organic (F/H) material and 3.7, 5.5 and 5.6, respectively for mineral soil (Bewley and Parkinson 1984).

Figure 3. Location of the study sites (circles) and associated sulphation and hydrogen sulphide exposure stations (squares) in relation to the West Whitecourt sour gas plant and conceptual sulphur gas emission corridor. Adapted from Legge and Bogner (1982).



METHODS

Respiration

a) Field Measurements of CO_2 Efflux

Measurements of *in situ* respiration were made at monthly intervals during the snow-free season of 1982 (May - October). At 10 random locations at each site, all green shoots were cut, and a plastic vial (height 6 cm, diameter 5 cm, surface area 19.6 cm^2) containing 10 mL of 1 N NaOH was uncapped and placed on the litter surface. Closed polyvinylchloride chambers (height 23 cm, diameter 27 cm, surface area 415.5 cm^2), were inverted over each vial and embedded in the soil to a depth of 6 cm. Three similar chambers not open to the soil were also placed randomly at each site, as controls. All chambers were covered with aluminum foil to prevent artificial heating. Thermometers were placed inside randomly-selected control and experimental chambers, and also in the ambient air, to check for temperature differences. Chambers were left in place for 24 hours (Witkamp 1969), after which time they were removed and the vials containing NaOH were capped and returned to the laboratory. CO_2-C content of the samples was determined by the titration method of Jenkinson and Powlson (1976), within 24 hours of return, and data were converted to mg CO_2 evolved m^{-2} hr^{-1}.

Values for average respiration rates on a total dry mass or organic mass basis were determined using data for weights of forest floor samples collected from other locations at each site at the same time as respiration measurements were taken. Forest floor samples were dried at 80°C for 24 hours, weighed, ground to a homogeneous state, ashed at 400°C for 24 hours, and reweighed, in order to determine the dry weight and weight of organic matter of the forest floor at each site. In June 1982, organic layers of the forest floor beneath each chamber were removed immediately following CO_2 efflux measurements. Dry mass and organic mass of these samples was determined, allowing for statistical comparison of respiration rates at each site on a mass basis.

Air temperature and precipitation data from Whitecourt Airport (28 km east of the study area), and soil temperature and snow depth data from Edson, Alberta (70 km south) for the period January 1982 - December 1983 were provided by Atmospheric Environment Service, Environment Canada, Edmonton, and used in the interpretation of field respiration data.

b) Laboratory Measurements of O_2 Uptake

After chambers were removed, a 10 cm diameter core of litter (L), fermentation (F), humus (H) and mineral soil (0-5 cm) material was taken from beneath each of the 10 chambers at each site. Each sample was separated into layers

and allowed to equilibrate at 22°C for 24 hours. Samples were then remoistened for 24 hours. 0.5 g of L needles were soaked in distilled water, 1.0 g of F needles were sprayed with water and kept in a closed petri dish, water was added to flasks containing variable amounts of humus, and 15 g (dry weight) of mineral soil were seived through a 2 mm mesh and remoistened to field capacity as determined on a pressure plate extractor. After 24 hours, samples were placed in flasks (Parkinson and Coups 1963) and equilibrated at 22°C in Gilson respirometers for 1 hour before oxygen uptake measurements were initiated. Respiration rates were determined as the mean value of three hourly measurements for each sample. Samples were then dried at 80°C for 24 hours, weighed, ashed at 400°C for 24 hours, and reweighed. Thus dry mass, organic matter content and mass, and original and remoistened moisture contents (dry mass basis) were determined. Respiration rates were expressed as uL O_2 g^{-1} dry mass or organic mass hr^{-1}.

Mass Loss

a) Litterbags

Senescent, brown pine needles remaining on trees were collected at each site on 25 January 1982, and air-dried for about 3 months. 2.0 grams of whole dried needles were placed in each of 300 10 X 20 cm litterbags constructed of

1 mm nylon mesh and polyester thread. Sixty bags were placed at the site from which the needles originated in order to determine differences in rates of weight loss of "endemic" needles at the 3 sites. An additional 60 bags containing needles from the most and least polluted sites were placed at the least and most polluted sites, respectively. These "exchanged" needles allowed for differentiation between effects due to altered properties of the needles as compared with those resulting from alterations in the decomposer communities at the polluted sites. Litterbags were labelled with numbered metal tags and transported to and from the field in envelopes and plastic bags to prevent spillage (Suffling and Smith 1974) and moisture loss. In May 1982, the bags were placed on the litter surface at 60 randomly selected points at each site. Where litter from two sites was used, one bag of each litter type was placed at each point. Twenty bags of each litter type were retrieved from each site after 5, 12 and 17 months, and returned to the laboratory for analysis. Needles were removed from the bags and washed to remove accumulated debris. 0.5 g from each bag were remoistened by soaking in a petri dish of water for 24 hours, and then measured for oxygen consumption on a Gilson respirometer. The remainder was dried at 80^{o}C for 24 hours reweighed, and converted to air dry mass using a correction factor of 4.6%. Needles used for respiration

measurement were weighed following remoistening and also following drying. In this manner, dry weight (hence weight loss), original and saturated moisture contents, and potential respiration rates were determined for needles from each site. Subsamples of needles from each litterbag were ashed at 400°C for 24 hours to determine organic mass remaining.

b) Litter bundles

Bundles of tethered pine needles were also employed in order to determine the effects of the artificial environment created by litterbags on decomposition rates (Anderson 1973; Gosz et al. 1973; Witkamp and Olson 1963). Thirty bundles composed of 1.0 g of indigenous pine needles sewn together at the petioles with nylon thread were placed at the most and least polluted sites at stakes having bags of each litter type. Transport, placement, retrieval and analyses of bundles were performed according to the techniques and schedules used for litterbags. Losses of entire needles were considered to be the result of the tethering procedure, thus a correction factor equal to the number of needles lost times the average weight of the needles at the time of retrieval was added to the total weight of the bundle. Loss of fragments was considered to be the result of decomposition and was not corrected for as the weight of fragments cannot be accurately estimated (Witkamp and Olson 1963).

Decomposition constants (k) were calculated for each set of litterbags and bundles using the equation: ln (final mass/initial mass) = -kt, where t is the time in years and k is the annual fractional loss (Olson 1963).

Litter Turnover

a) Litterfall

Falling litter was trapped in 15 plastic buckets 45 cm in diameter and 45 cm high at each site. Polyethylene bags perforated to allow drainage of water were placed in each bucket. Litter in all traps was collected at the middle of each month from May 1982 to December 1983, except for occasional bimonthly collections. Upon return to the laboratory, litter was washed, dried (80^{o}C for 24 hours), sorted into components, and weighed to determine total litterfall and proportions of litter materials at each site. Random samples were ashed at 400^{o}C for 24 hours to determine organic matter content of litterfall. Litterfall was expressed as g dry mass or organic mass m^{-2}. To demonstrate seasonal patterns, litterfall data were corrected for 30 day months. Annual litterfall for each site was calculated as the mean of totals from all traps for which complete data sets existed from January to December 1983.

b) Litter Accumulation

Litter standing crop was estimated from the weight of

cores of the organic layers at each site. Fifteen random 15 cm diameter cores were taken from each site at monthly intervals from May-October 1982, and May-June 1983. Cores were separated into L, F, and H layers (according to Kendrick and Burges 1962); L and F layers were washed, all layers were then dried at 80°C for 24 hours. Following dry weight determination, F and H material was ashed at 400°C for 24 hours to determine organic matter content of samples. Litter material was sorted into various constituents, and random samples were ashed to determine organic matter content of litter. Litter standing crop was expressed as g dry mass or organic mass m^{-2}. Measurements of forest floor depth from surface to mineral soil were made before removal of cores in May and June of 1983.

c) Litter Residence Times

Organic matter residence times were calculated using ratios of average forest floor mass to total annual litterfall using the equation $t = H/L$, where t is the turnover time in years, H is the forest floor mass, and L is annual litterfall mass (Gosz et al. 1976). Values for annual fractional turnover of forest floor organic matter were determined as the reciprocal of turnover times (Vogt et al. 1983).

Statistical Tests

All differences between sites or between sample times

were tested for significance with a oneway analysis of variance (ANOVA) and Scheffe multiple range test. Comparisons involving both site and time (forest floor mass and field respiration) were tested with twoway ANOVAs. Percentage data were first transformed with logarithmic or arc sin transformations. Data sets determined to have non-homogeneous variances in a Bartlett-Box F test were analyzed with a Kruskall-Wallis nonparametric test and post-hoc test. Correlation coefficients were determined to investigate relationships between temperature, moisture and respiration, forest floor depth and mass, and litterbags and bundles. Differences between two means (litterbags and bundles, 1982 and 1983 litterfall) were analyzed with t-tests. Bivariate data with non-normal distribution were tested with Spearman Rank Correlations. Unless otherwise stated, the accepted level of significance was $p<0.05$.

RESULTS

Respiration

a) Field Measurements of CO_2 Efflux

Respiration rates of undisturbed profiles did not differ between sites on any sampling occasion on an areal (m^{-2}) basis (Figure 4). However, when rates were expressed on the basis of dry or organic mass (Figure 4), respiration was always lower at the most polluted site (1) than at the least polluted site (3). Respiration rates for the June 1983 samples, for which the organic layers beneath the chambers were used to determine rates on a mass basis, showed a similar trend which was significant (Figure 4).

In situ respiration rates were lowest in May and October, and peaked in August. Soil temperature was also lowest in May and October and highest in June and July (Figure 2). Precipitation was high in June and July and low in May, September and October (Figure 2). Moisture content of organic layers was greatest in August and low in June and September (Figure 5). Sites were similar with respect to temperature and moisture content at sample times. Coefficients of variation for field respiration measurements averaged 19 per cent (m^{-2}) and 32 per cent (g organic $mass^{-1}$).

b) Laboratory Measurements of O_2 Uptake

Basal respiration rates of separated L, F, H and mineral soil samples were also lowest at site 1 and highest at site

Figure 4. *In situ* respiration rates from the forest floor at 3 sites located (1) 2.8 km, (2) 6.0 km, and (3) 9.6 km from a sour gas plant emitting SO_2. Mean and standard errors are indicated. Sites with the same letter do not differ significantly at $p \leq 0.05$.

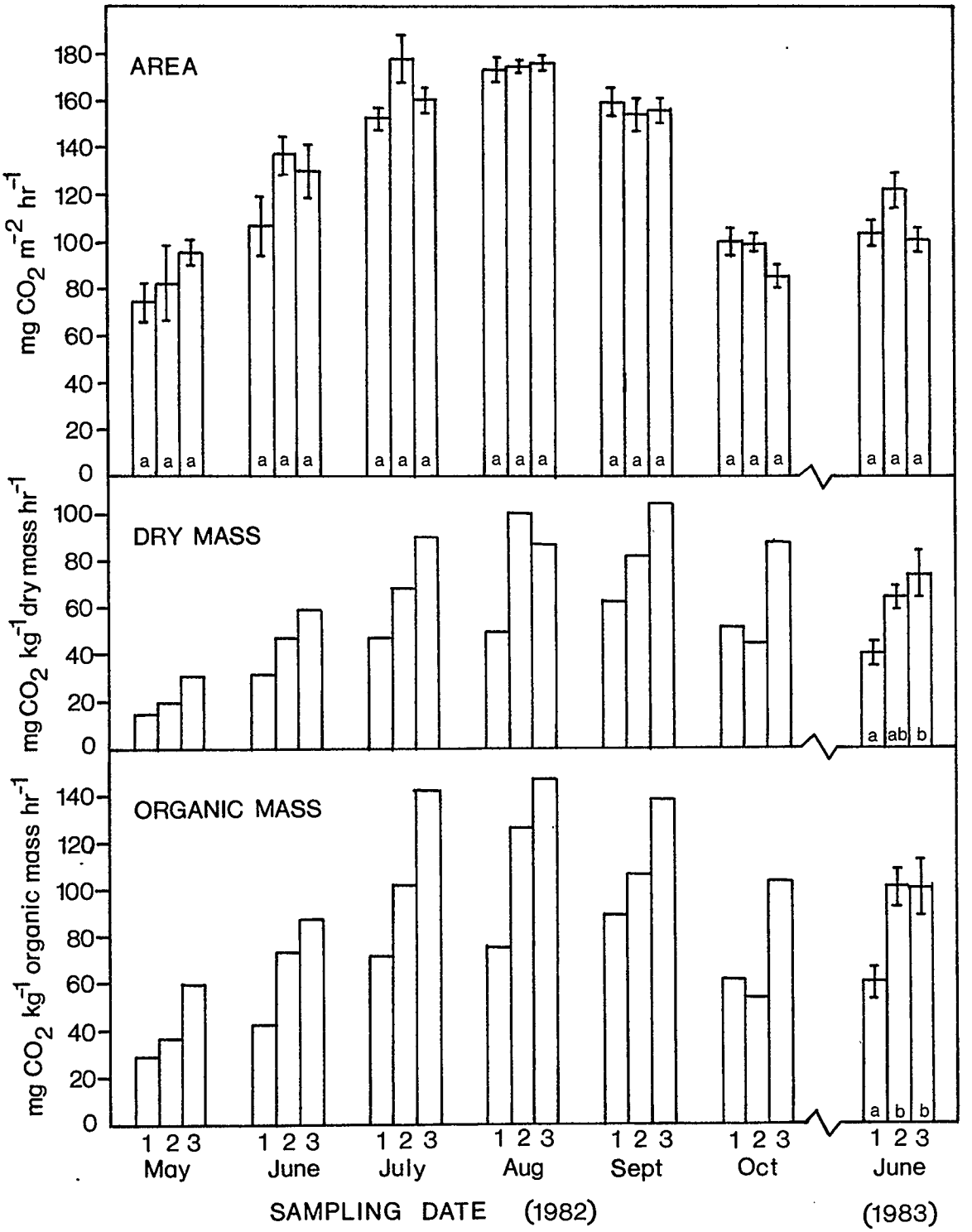
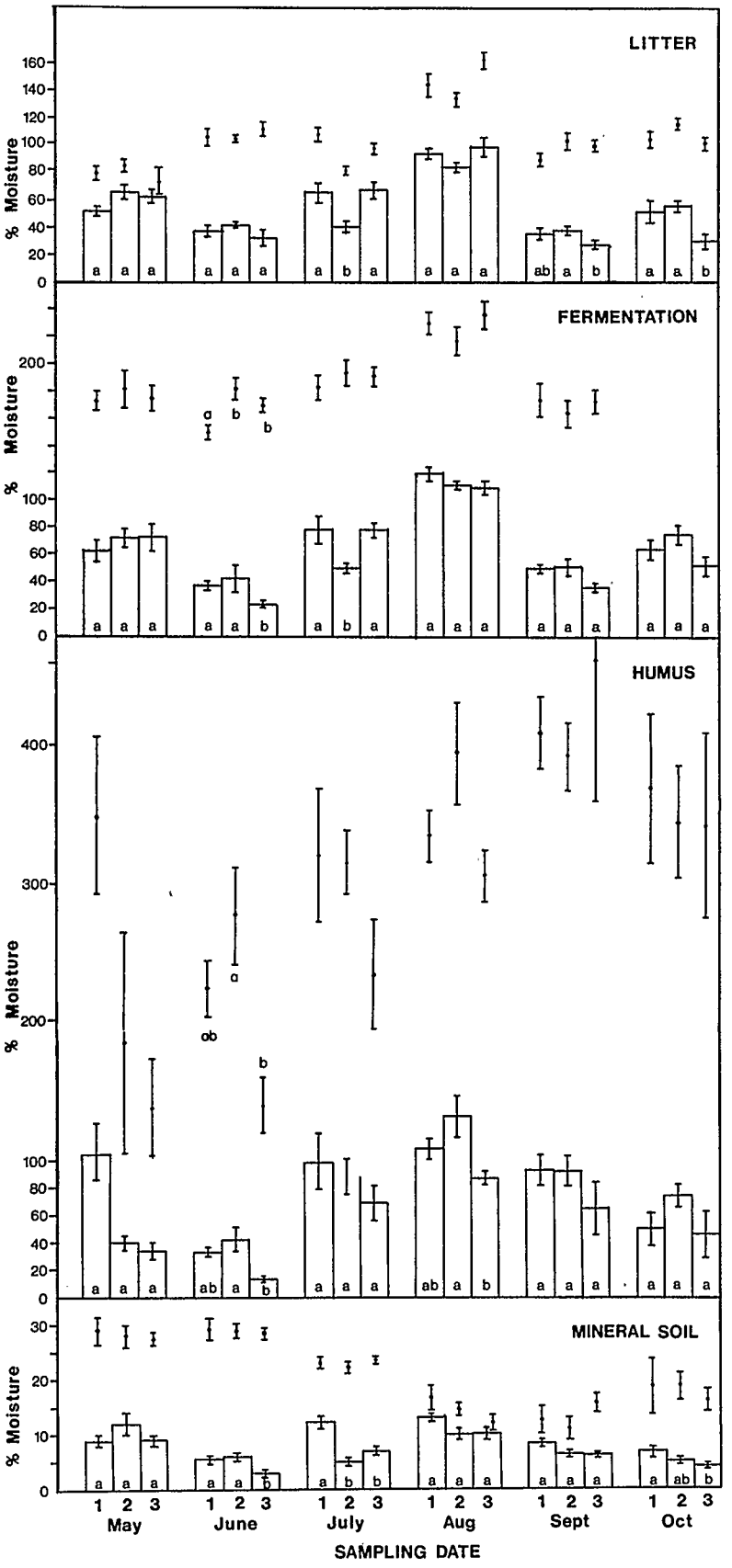

AREA
mg CO_2 m^{-2} hr^{-1}
DRY MASS
mg CO_2 kg^{-1} dry mass hr^{-1}
ORGANIC MASS
mg CO_2 kg^{-1} organic mass hr^{-1}
1 2 3
May
June
July
Aug
Sept
Oct
June
SAMPLING DATE (1982) (1983)

Figure 5. Moisture content of forest floor organic and mineral layers at the 3 sites before (histograms) and after (dots) remoistening. Mean and standard errors are indicated. Sites with the same letter do not differ significantly at $p \leq 0.05$. Unless otherwise indicated, moisture content following remoistening are similar at the 3 sites.


LITTER
FERMENTATION
HUMUS
MINERAL SOIL
% Moisture
1 2 3
May
June
July
Aug
Sept
Oct
SAMPLING DATE

3 (Figure 6). Needles from the litter layer at site 3 consistently respired faster than those from site 1; this trend was significant from July through October. Respiration of needles from the fermentation layer was significantly lower at site 1 than at sites 2 or 3 on every sampling occasion. Respiration of humus samples was highly variable, especially at site 3 where samples were smaller both in number and in mass. Rates from sites 2 and 3 did, however, tend to be higher than those from site 1. Mineral soil samples from site 1 respired at a lower rate than those from sites 2 and 3 on three occasions, but were similar at other times.

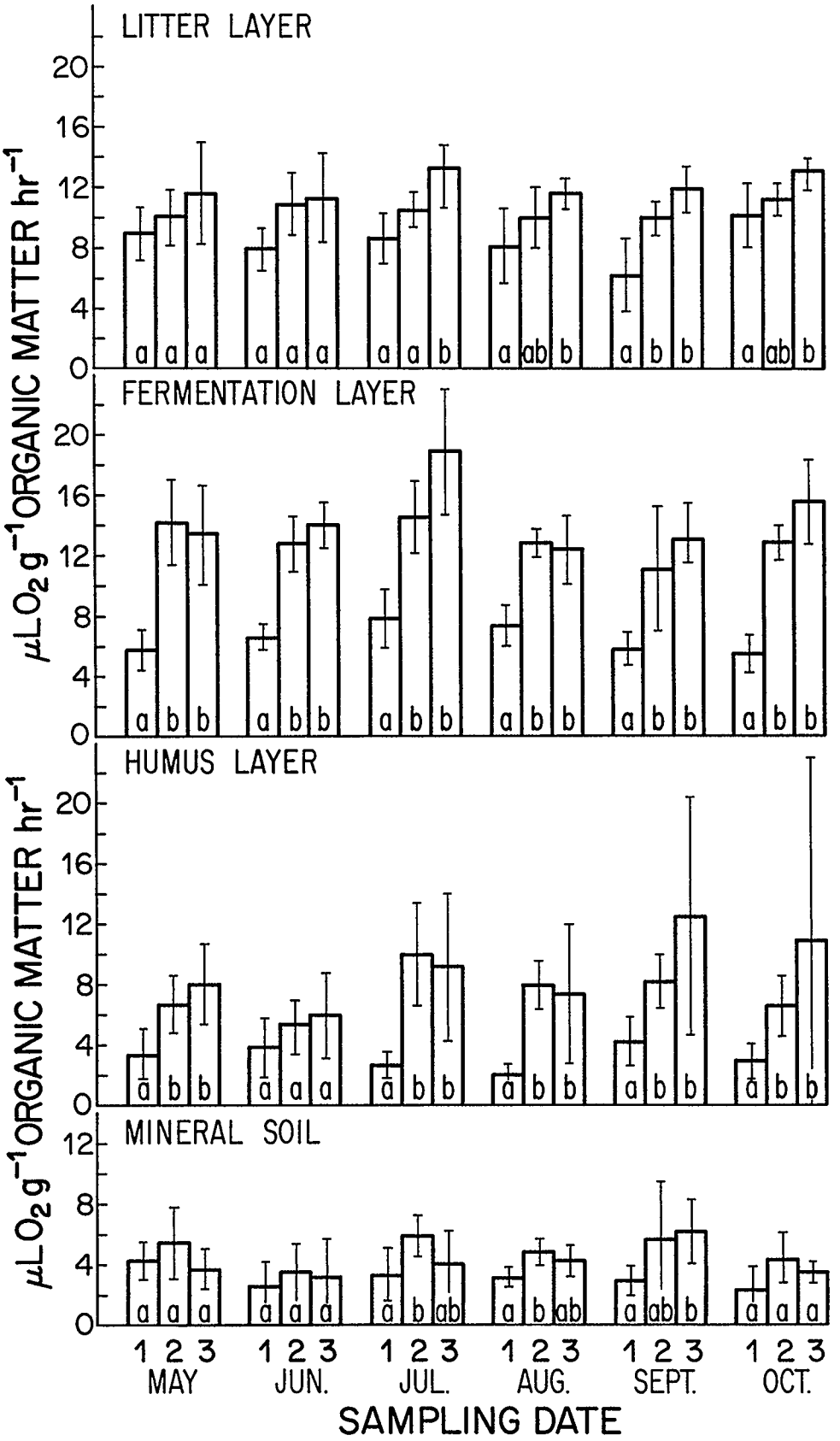
The fermentation layer displayed the highest respiration rates; followed in order of decreasing rates by litter, humus and mineral soil. There were no significant differences in basal respiration rates of remoistened samples of any layer from any site between the 6 sample dates. Basal respiration rates did not correlate with either temperature or moisture levels alone. Average coefficients of variation for basal respiration were L - 23%, F - 24%, H - 43%, mineral soil - 50%.

Mass Loss

a) Litterbags

Mass loss of endemic needles in litterbags was lower

Figure 6. Basal respiration rates of separated organic and mineral layers of the forest floor at the 3 sites. Mean and 95% confidence intervals are indicated. Sites with the same letter do not differ significantly at $p \leq 0.05$.


LITTER LAYER
FERMENTATION LAYER
HUMUS LAYER
MINERAL SOIL
μL O2 g-1 ORGANIC MATTER hr-1
0
4
8
12
16
20
a a a a a a a a b a ab b a b b a ab b
a b b a b b a b b a b b a b b a b b
a b b a a a a b b a b b a b b a b b
a a a a a a a b ab a b ab a ab b a a a
1 2 3 MAY
1 2 3 JUN.
1 2 3 JUL.
1 2 3 AUG.
1 2 3 SEPT.
1 2 3 OCT.
SAMPLING DATE

at site 1 than at sites 2 and 3 over the 17 months (Figure 7). This trend occurred during both summers; mass loss rates were low at all sites during the winter (October to May). Mass loss over the first year amounted to 10.5% at site 1 and 12.5% at the other sites (Table 1). Decomposition during the second summer was slightly lower than that during the first summer. Annual decay constants are also shown in Table 1. Basal respiration of endemic needles in litterbags was also lower at site 1 than at the other sites (Figure 7), even in the undecomposed (Time 0) needles. Respiration rates of needles at all sites increased during the first 5 months of decomposition and were similar thereafter.

b) Exchanged Litterbags

Needles in exchanged litterbags (1 at 3 and 3 at 1) decomposed and respired at rates intermediate to the non-exchanged needles (1 at 1 and 3 at 3) (Table 1, Figure 8). Needles originating from site 1 lost less mass over the first summer (0-5 months) than did needles from site 3, regardless of site of placement. Over the second summer (12-17 months), needles at site 3 decomposed faster than those at site 1, regardless of site of origin. Site 1 needles decomposed at site 3 had respiration rates similar to 3 at 3 needles, and higher than 1 at 1 needles (Figure 8). Similarly, site 3 needles decomposed at site 1 respired

Figure 7. Mass loss and basal respiration rates of endemic pine needles decomposed in litterbags at the 3 sites for 17 months. Mean and standard errors are indicated. Sites with the same letter do not differ significantly at $p \leq 0.05$.

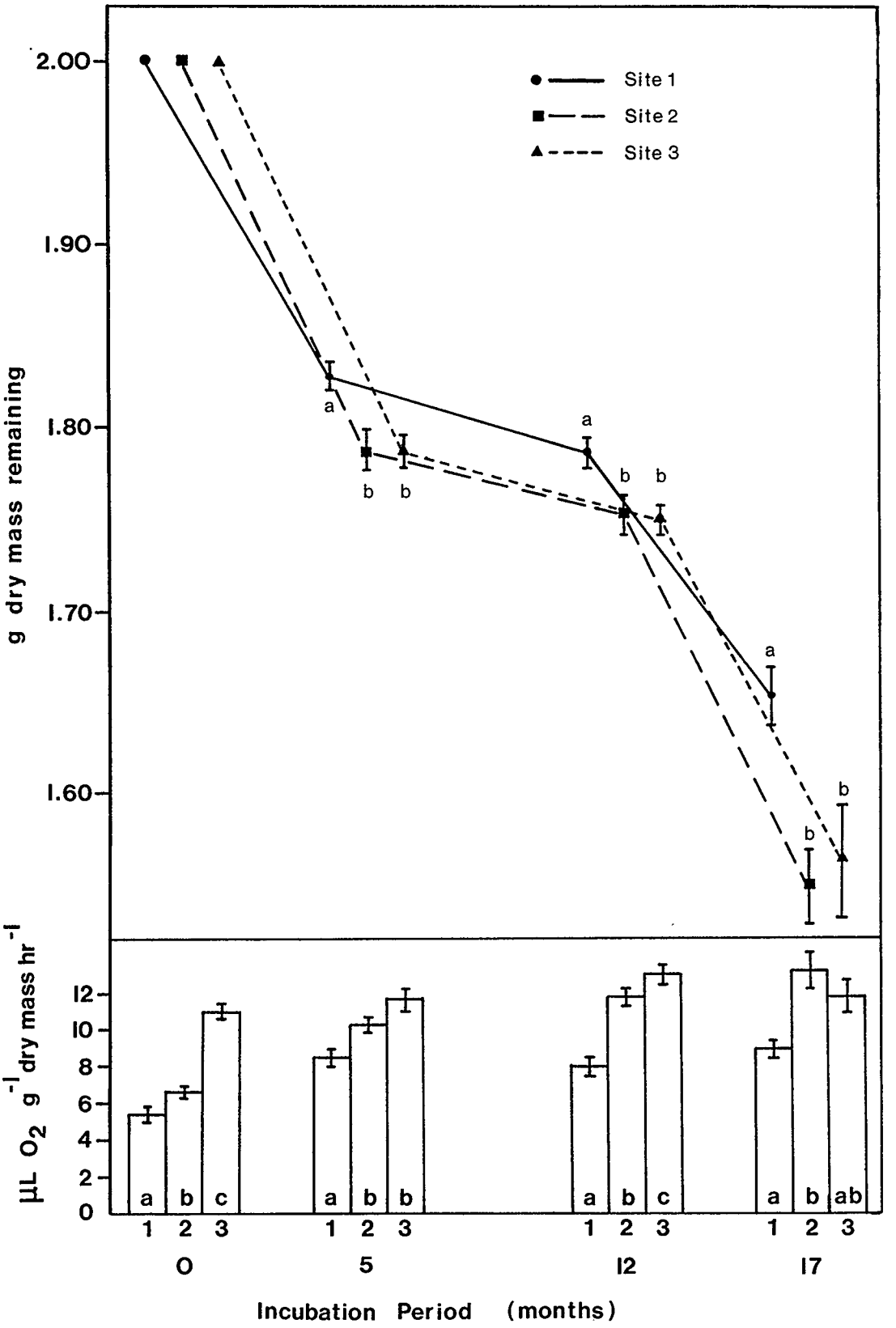

Site 1
Site 2
Site 3
g dry mass remaining
2.00
1.90
1.80
1.70
1.60
a
b
b
a
b
b
a
b
b
µL O2 g-1 dry mass hr-1
12
10
8
6
4
2
0
a b c
a b b
a b c
a b ab
1 2 3
0
5
12
17
Incubation Period (months)

Table 1. Decomposition rates of pine needles in litterbags and bundles at 3 sites located (1) 2.8 km, (2) 6.0 km, and (3) 9.6 km from a sour gas plant emitting SO_2.

Enclosure Type	Site [1]			% of Dry Mass Lost During Each Interval [2]				Annual Fractional Loss (k) [3]		
	Origin	Decomposition		0 - 5	5 - 12	12 - 17	0 - 17	0 - 12	5 - 17	0 - 17 [4]
Bag	1	at	1	8.5	2.0	7.0	17.5	0.11	0.10	0.11
	2	at	2	10.5	2.0	10.0	22.5	0.13	0.14	0.14
	3	at	3	10.5	2.0	9.5	22.0	0.13	0.13	0.13
	3	at	1	11.5	1.0	7.0	19.5	0.13	0.10	0.11
	1	at	3	8.5	2.5	8.0	19.0	0.12	0.12	0.12
Bundle	1	at	1	12.0	1.0	12.0	25.0	0.14	0.16	0.15
	2	at	2	15.0	1.0	10.0	26.0	0.17	0.14	0.15
	3	at	3	13.0	3.0	6.0	21.0	0.17	0.10	0.13

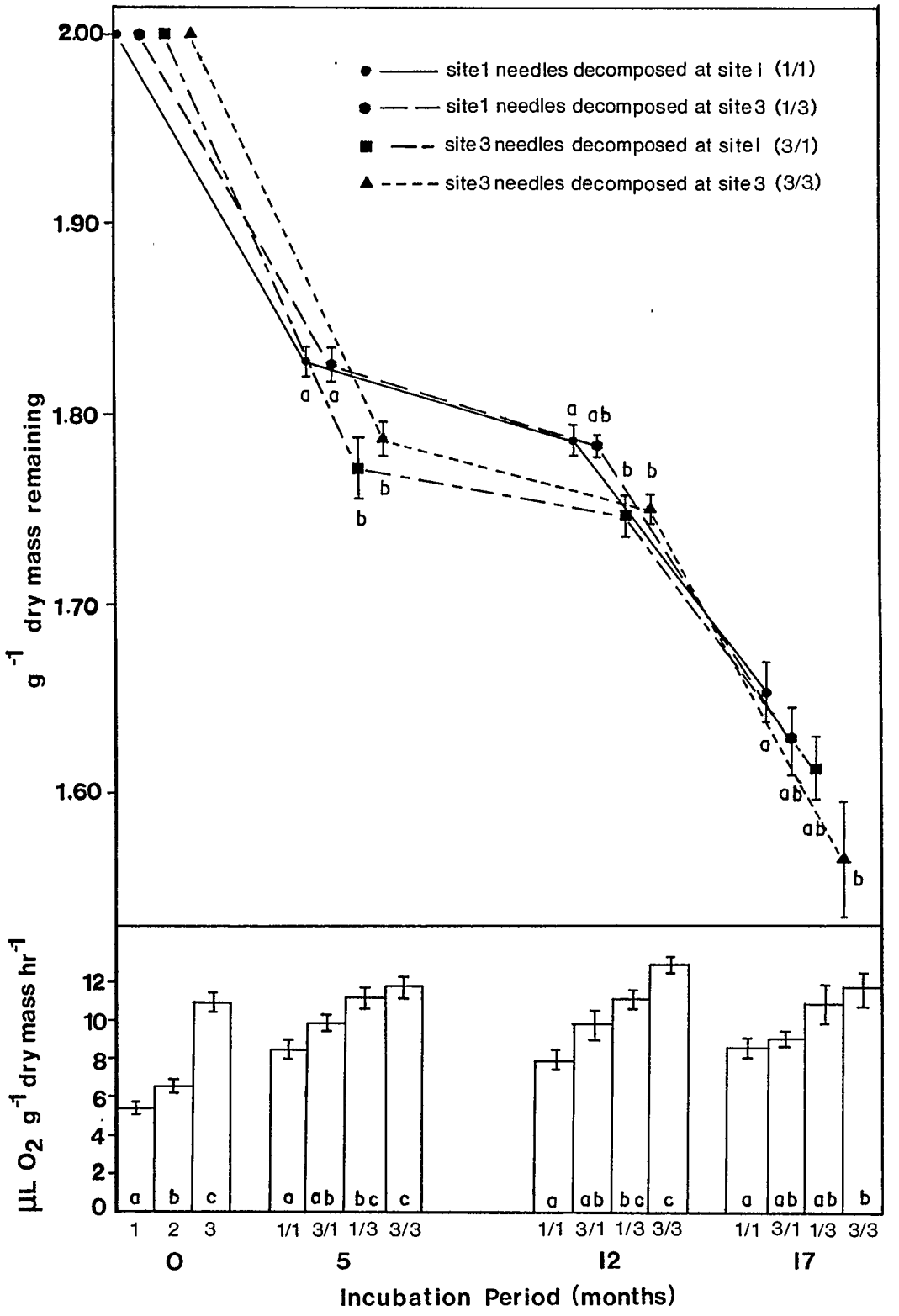
[1] *eg. 1 at 3 = needles originating from site 1 decomposed at site 3.*

[2] *Intervals: 0 - 5 months = May 1982 - Oct 1982*
5 - 12 months = Oct 1982 - May 1983
12 - 17 months = May 1983 - Oct 1983

[3] $\ln \left[\frac{\text{final mass}}{\text{initial mass}} \right] = -kt$
(Olson 1963)

[4] *mean of 0-12 and 5-17 k values.*

Figure 8. Mass loss and basal respiration rates of endemic and exchanged pine needles decomposed in litterbags at the 3 sites for 17 months. Mean and standard errors are indicated. Sites with the same letter do not differ significantly at $p \leq 0.05$.


site1 needles decomposed at site 1 (1/1)
site1 needles decomposed at site3 (1/3)
site3 needles decomposed at site1 (3/1)
site3 needles decomposed at site3 (3/3)
2.00
1.90
1.80
1.70
1.60
g -1 dry mass remaining
µL O2 g -1 dry mass hr -1
12
10
8
6
4
2
0
1 2 3 1/1 3/1 1/3 3/3 1/1 3/1 1/3 3/3 1/1 3/1 1/3 3/3
0 5 12 17
Incubation Period (months)

at rates similar to 1 at 1 needles, and lower than 3 at 3 needles.

c) Litter Bundles

Due to the large variability of data from the bundles, no significant differences were determined for weight loss of endemic needles in bundles at the 3 sites (Figure 9). Respiration of bundle needles tended to increase with distance from the plant, and also over the first 5 months at each site, however these data were also more variable than those from litterbags (Figure 9).

Needles in bundles decomposed significantly faster than those in bags and showed similar seasonal trends, but did not differ in respiration rates (Table 2). They also took up more water upon remoistening and had lower original moisture contents on one occasion (May 1982). Needles in bags and bundles decomposed at the same stake were related in terms of original moisture content, but not in decomposition or respiration rates. Average coefficients of variation were 4% (bags) and 6% (bundles) for dry mass remaining, and 22% for basal respiration of needles in both bags and bundles. Organic matter content of needles from site 1 (95.8%) was significantly lower than that of needles from sites 2 and 3 (97.3%) throughout the 17 months, regardless of site of placement.

Figure 9. Mass loss and basal respiration rates of endemic pine needles decomposed in litter bundles at the 3 sites for 17 months. Mean and standard errors are indicated. Sites with the same letter do not differ significantly at $p \leq 0.05$.

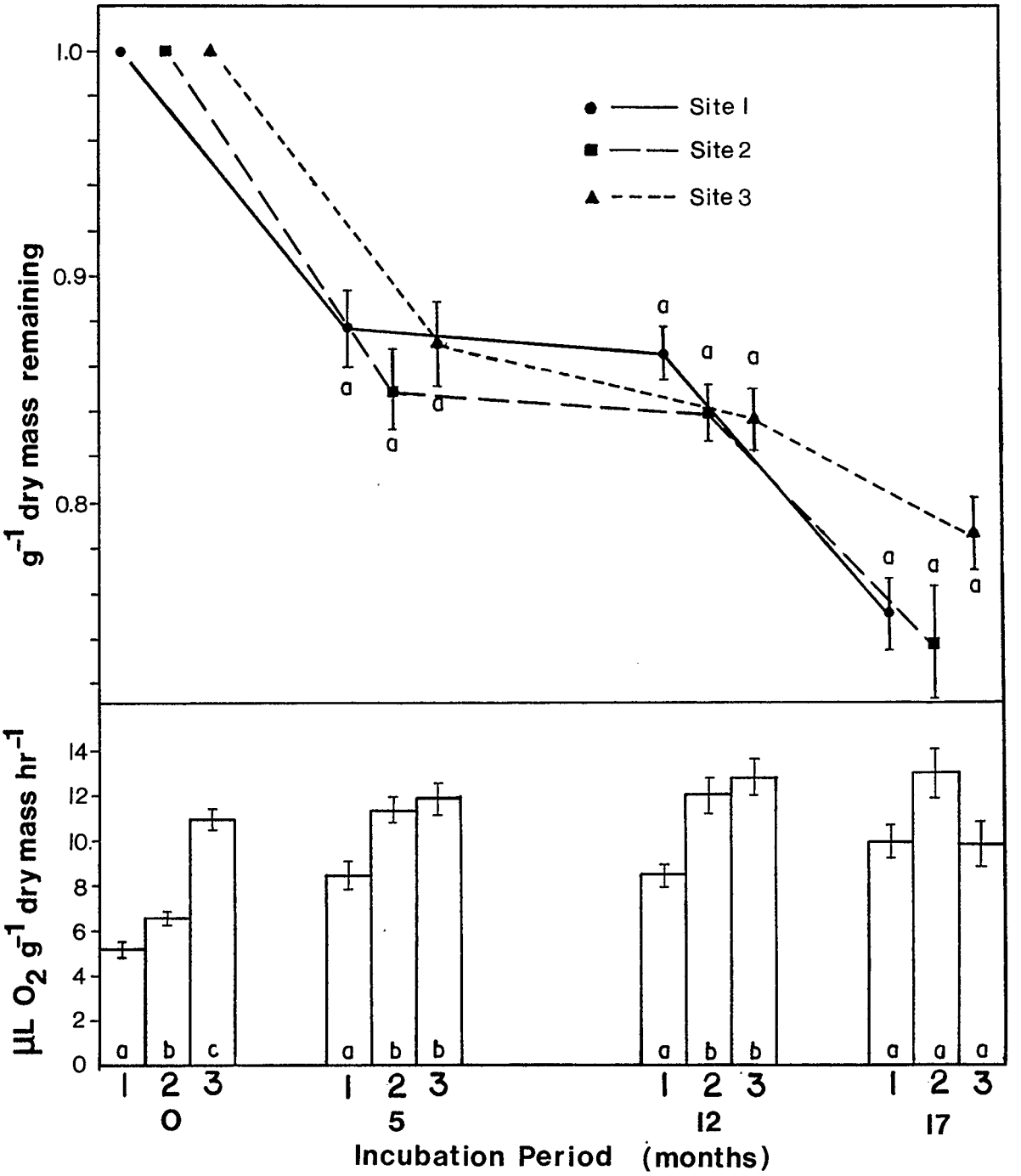

1.0
0.9
0.8
g⁻¹ dry mass remaining
Site 1
Site 2
Site 3
a
a
a
a
a
a
a
a
a
14
12
10
8
6
4
2
0
µL O2 g⁻¹ dry mass hr⁻¹
a b c
a b b
a b b
a a a
1 2 3
1 2 3
1 2 3
1 2 3
0
5
12
17
Incubation Period (months)

Table 2. Comparison of needles decomposed in litterbags and bundles for 17 months. Means and standard errors for 24 bag-bundle pairs[1] from all 3 sites are indicated. Sets with the same letter do not differ significantly at $p \leq 0.05$.

Enclosure Type	Mass Remaining (g)	Moisture Content		Respiration Rate
		Original %	Remoistened %	$\mu L\ O_2\ g\ dry\ mass^{-1}\ hr^{-1}$
bag	0.76 ± 0.01 a	16.76 ± 0.30 a	149.86 ± 4.60 a	11.14 ± 0.82 a
bundle	0.72 ± 0.01 b	16.30 ± 0.48 a	170.49 ± 7.04 b	11.05 ± 0.67 a
Correlation:[2]				
r	-0.12	0.74	0.42	0.34
p	0.56	0.0001	0.04	0.11

[1] *i.e. needles from 1 bag and 1 bundle decomposed at the same stake*

[2] *Pearson correlation coefficients and probabilities for bag-bundle pairs*

Litter Turnover

a) Litterfall

Annual litterfall mass was greatest at site 2 and least at site 3 (Table 3). Although the trees at site 3 were larger than those at site 1, almost a third of the plot at site 3 was open, which led to the low values for stand density and basal area at this site (Table 3). As a result, litterfall mass per cm^2 basal area was similar at all sites (Table 3). Seasonal patterns of litterfall were similar at the three sites, with autumn peaks and winter lows (Figure 10). A spring peak was observed in May and June of 1983, but not in 1982 (sampling did not commence until June in 1982). Litterfall from June to December was greater in 1982 at site 1, greater in 1983 at site 2, and similar both years at site 3.

Litterfall was predominantly (91-94%) composed of pine needles at all sites (Table 4). Relative proportions of cones, branches, bark and aspen leaves were similar when averaged over all 3 sites, but differed among sites. Site 1 had proportionately more branch litter, site 2 had more cones and aspen leaves, and site 3 had more bark. Cone fall peaked in summer, aspen leaf fall occurred only in autumn, and branch and bark fall was highly irregular. Coefficients of variation for total litterfall were 20% for annual totals and 42% for monthly totals. Needlefall coeffi-

Table 3. Annual (1983) litterfall at the 3 sites. Means and standard errors are indicated. Sites with the same letter do not differ significantly at $p \leq 0.05$.

Site	n	Litterfall Mass[1] g^{-1} OM m^{-2} yr^{-1}	Tree Density (stems ha^{-1})	Mean dbh (mm)	Stand Basal Area (m^2 ha^{-1})	Litterfall Mass g OM cm^{-2} basal area
1	13	137.69 ± 7.60 ab	8725	56.16 ± 1.17 a	28.15	5.04 ± 0.28 a
2	14	147.55 ± 6.63 a	5639	68.17 ± 1.84 b	27.23	5.58 ± 0.25 a
3	11	112.22 ± 7.69 b	3962	71.78 ± 2.24 b	20.97	5.52 ± 0.38 a

[1] *OM = organic matter*

Figure 10. Seasonal patterns of litterfall at the 3 sites for the period 17 May 1982 - 17 December 1983. Mean and standard errors are indicated. Sites with the same letter do not differ significantly at $p \leq 0.05$. All samples were collected at mid-month and data are corrected for 30 day months. For bimonthly collections, data for each month are expressed as one-half of the two-month total.

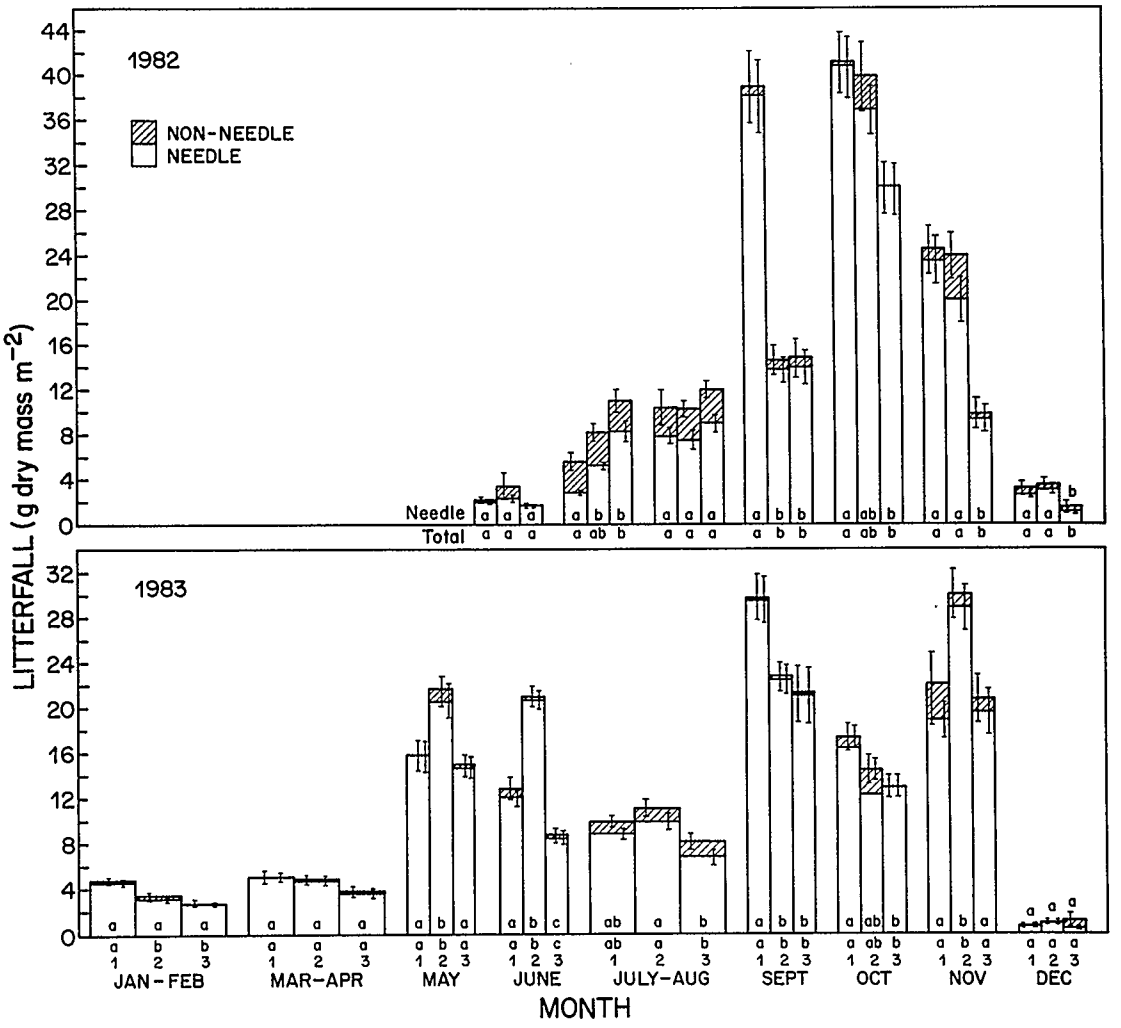


Table 4. Composition of litterfall at the 3 sites. Means and standard errors from 1983 annual litterfall are indicated. Sites with the same letter do not differ significantly at $p \leq 0.05$. Top number is mass of material in litterfall in g m^{-2}, number in brackets is percent of the total litterfall which the material comprises.

Material	Site 1	Site 2	Site 3	Average
pine needles	128.59 ± 5.52 ab (93.4%)	138.39 ± 6.07 a (93.8%)	102.45 ± 8.52 b (91.4%)	92.9%
pine cones	2.46 ± 0.43 a (1.8%)	4.59 ± 0.68 b (3.1%)	2.94 ± 0.76 a (2.6%)	2.5%
branches	6.46 ± 2.93 a (4.7%)	0.43 ± 0.20 b (0.3%)	4.24 ± 2.00 a (3.8%)	2.9%
bark	0.23 ± 0.09 a (0.2%)	0.20 ± 0.09 a (0.1%)	2.50 ± 1.28 b (2.2%)	0.8%
non-pine vegetation	0.32 ± 0.12 b (0.2%)	3.68 ± 0.95 c (2.5%)	0.00 ± 0.00 a (0.0%)	0.9%
n	13	14	11	

cients of variation were 20% (annual) and 37% (monthly). Coefficients of variation for annual totals of other litterfall components were: cones 68%, branches 145%, bark 160% and aspen leaves 116%.

b) Litter Accumulation

Forest floor dry mass and organic mass were greatest at site 1 and least at site 3 on every sampling occasion (Figure 11). These differences were significant on 7 of the 8 occasions. Total forest floor mass decreased significantly between May and October (Figure 11). Relative masses of the 3 sites were similar at all times, hence data for all months were pooled to determine average forest floor mass at each site (Table 5). Average forest floor mass decreased significantly with distance from the gas plant.

Mass of each layer of the forest floor was greatest at site 1 and least at site 3 (Table 5). The proportional distribution of mass between the 3 layers was similar at all sites, averaging 82% fermentation, 9% litter and 9% humus. However, there was very little humus, hence proportionately more fermentation material at site 3. Depth of the forest floor from surface to mineral soil was also greatest near the gas plant, averaging 45 mm at site 1, 36 mm at site 2, and 27 mm at site 3. Depth correlated with both dry mass and organic mass of forest floor samples.

Figure 11. Forest floor organic mass at the 3 sites. Mean and standard errors are indicated. Sites with the same letter do not differ significantly at $p \leq 0.05$.

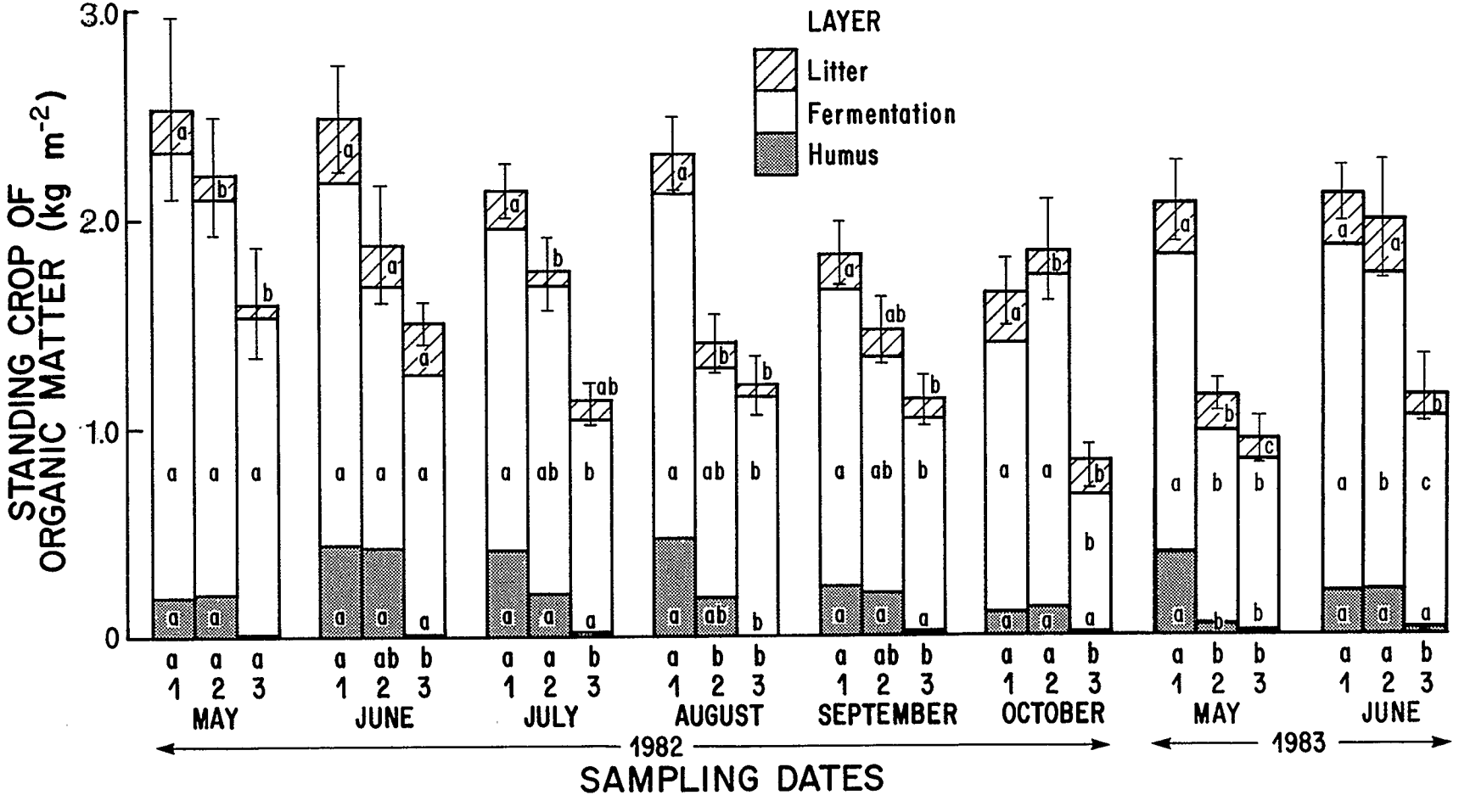


Table 5. Distribution of forest floor mass among organic layers at the 3 sites. Means and standard errors of 8 sample sets (May - Oct 1982, May - June 1983) are given. Sites with the same letter do not differ significantly at $p \leq 0.05$.

Layer	Site	n	Dry Mass			Organic Matter Content	Organic Mass		
			$g\ m^{-2}$		Distribution		$g\ m^{-2}$		Distribution
total L+F+H	1	112	3052.0 ± 140.2	a		67.8%	2111.3 ± 71.6	a	
	2	115	2405.5 ± 119.9	b		69.0%	1697.6 ± 80.0	b	
	3	119	1758.0 ± 93.0	c		65.4%	1182.0 ± 55.9	c	
L	1	113	224.2 ± 9.8	a	7.4%	95.2%	213.1 ± 9.3	a	10.2%
	2	118	146.7 ± 9.4	b	6.1%	94.4%	138.5 ± 8.8	b	8.2%
	3	120	110.2 ± 8.1	c	6.3%	94.3%	104.0 ± 7.6	c	8.8%
F	1	112	2149.8 ± 99.0	a	71.2%	72.0%	1579.1 ± 63.3	a	75.4%
	2	115	1894.9 ± 96.4	ab	78.8%	70.0%	1356.4 ± 62.4	b	80.0%
	3	119	1620.0 ± 90.8	b	92.5%	64.1%	1069.3 ± 54.7	c	90.4%
H	1	112	643.9 ± 94.0	a	21.3%	46.6%	300.8 ± 42.2	a	14.4%
	2	115	363.3 ± 62.2	b	15.1%	54.6%	201.6 ± 36.6	a	11.9%
	3	119	20.4 ± 7.2	c	1.2%	39.0%	99.2 ± 2.8	b	0.8%

Pine needle litter comprised an average of 82% of the mass of the litter layer; pine cones, branches, bark, wood, non-pine vegetation and faecal material contributed similar proportions of the remainder (Table 6). Relative proportions of all materials were similar at the 3 sites, except for branch litter which was proportionately more abundant at site 1. Coefficients of variation for samples of forest floor organic mass averaged: litter 50%, fermentation 42%, humus 202%, total 33%.

c) Litter Residence Times

Residence times for organic matter were 9.3 years at site 3, 10.6 years at site 2, and 14.3 years at site 1. These values are for turnover of overstory litter only, as this was the only litter input measured, and were calculated by subtracting the proportion of litter in the L layer of non-overstory origin (wood, understory vegetation, faeces) from the total forest floor mass before calculating residence times. Without this correction, residence times would be overestimated by 6-12%.

Table 6. Composition of the litter layer at the 3 sites. Means and standard errors of 7 sample sets (May - Oct 1982, May 1983) are indicated. Sites with the same letter do not differ significantly at $p \leq 0.05$. Top number is mass of material in g m^{-2}, number in brackets is percent of total litter mass at that site which the material comprises.

Material	Site 1	Site 2	Site 3	Average
pine needles	168.52 ± 8.72 a (80.7%)	101.45 ± 6.78 b (83.7%)	80.17 ± 6.19 b (81.1%)	81.8%
pine cones	4.33 ± 2.03 a (2.1%)	2.96 ± 0.47 a (3.3%)	4.04 ± 1.96 a (5.0%)	3.5%
branches and bark	14.40 ± 1.91 a (6.7%)	2.49 ± 0.80 b (1.6%)	5.46 ± 1.62 b (4.0%)	4.1%
wood	3.98 ± 1.53 a (2.5%)	3.15 ± 1.49 a (2.4%)	5.88 ± 4.63 a (1.7%)	2.2%
non-pine vegetation	5.16 ± 0.09 a (3.0%)	5.21 ± 0.76 a (4.7%)	4.18 ± 0.58 a (5.6%)	4.4%
faeces	6.61 ± 1.07 a (3.1%)	3.67 ± 0.67 a (3.0%)	4.27 ± 0.94 a (3.1%)	3.1%
n	96	103	104	

DISCUSSION

Respiration

The lower potential and *in situ* respiration rates at site 1 as compared with the control site indicate a suppression of heterotrophic activity in the forest floor close to the gas plant. Given the ecological similarity of the three sites and the consistent correlation between distance from the plant and respiration rates, it is reasonable to conclude that the differences in respiration rates are related to sulphur loadings. Differences in rates of respiration of roots may be partially responsible for the differences in rates of *in situ* respiration at the 3 sites. Roots are known to be sensitive to pH levels and associated levels of metals and nutrients in the soil (Russell 1977). However, since similar trends were observed in material in which roots were not present (L and F) or had been removed (mineral soil), it is unlikely that root respiration was responsible for a significant proportion of the differences in respiration. Thus it appears that the differences in respiration rates between sites are primarily due to different levels of activity of soil organisms. The observation of similar trends in separated material from which macroscopic organisms had been largely removed, suggests that the observed suppression is occurring primarily at the microbial level.

Reduced rates of respiration have also been reported in soil acidified with elemental sulphur (Bryant et al. 1979) and dilute sulphuric acid (Baath et al. 1979) for several years. Results of short-term acidification experiments (Francis 1982, Hovland et al. 1980, Killham et al. 1983, Roberts et al. 1980) have been more variable, with reductions in respiration rates occurring only at very low pH levels.

The monthly trends observed in the field did not occur in samples of the same materials run at higher temperature and moisture levels, thus these factors were probably limiting in the field. Although respiration followed the same general trend as soil temperature, the correlation between the two factors was not significant. Comparison of soil temperature and in situ respiration rates showed respiration to be very low in May and October when soil temperature averaged 8.3°C and 7.0°C respectively, but higher and more variable at other times when the temperature was above 10°C. Thus temperature is probably the overriding factor in May and October when temperatures are around the 5°C critical level for microbial growth (Gray and Williams 1971). The peak in respiration in August, rather than in June or July when temperatures were higher but moisture levels lower, suggests an influence of moisture at these times. Litter moisture levels were below the critical level of 40 - 60% determined by Piene and Van Cleve (1976) for white spruce litter, in

June and September, and may have been limiting at these times. However, the high frequency of rain throughout the summer, and the finding of no significant plant moisture stress at the sites (Legge et al. 1978), suggest that moisture is only sporadically limiting in this system. The high rates of CO_2 evolution from the forest floor in September despite relatively cool and dry conditions may be reflective of the input of fresh litter at this time, as suggested by Witkamp (1966) and De Boois (1974). Similar stimulation of oxygen uptake in samples run under standardized conditions in the laboratory was, however, not observed at this time. Thus it appears that temperature sets the general level of activity in this system, by overriding other factors when temperatures fall to around $5^{o}C$. At higher temperatures, moisture fluctuations and changes in substrate quality may influence respiration rates. Similar conclusions have been reached by Anderson (1973), Cowling and MacLean (1981) and Witkamp (1966), and are characteristic of boreal forests (Swift et al. 1979). A more extensive examination with more frequent sampling or controlled conditions would be necessary to test these speculations.

Advantages and limitations of the inverted box and alkali absorption techniques have been discussed elsewhere (Mina 1962, Singh and Gupta 1977, Piene and Van Cleve 1976). The accuracy of respiration measurements from this method are

hampered by several complicating factors including root respiration, incomplete oxidation of carbon compounds, variable CO_2 diffusion rates (Piene and Van Cleve 1976), anaerobic respiration (Kucera and Kirkham 1971), inefficient absorption by alkali (Kirita and Hozumi 1966) and disturbance and enclosure effects (de Jong et al. 1979, Edwards 1982). Despite its limitations, the static chamber - alkali absorption technique is considered to be a simple and inexpensive method for determining relative rates of respiration (Reiners 1968) which involves minimal disturbance of the forest floor and can be used in remote areas (Edwards 1982, Singh and Gupta 1977). A number of specifications have been suggested for the inverted box - alkali absorption method: (1) the chamber must stand at least 8 cm above the litter surface and be embedded at least 5 cm, (2) the alkali surface must be at least 2.5 cm above the litter surface and have a surface area equal to at least 13% of the chamber surface area, and (3) at least 35% of the alkali must remain unconsumed (Singh and Gupta 1977). In the present investigation, the height and area of the alkali surface did not meet these specifications, which may have led to some underestimation of CO_2 evolution rates. However, the similarity of trends in the data acquired by this method and those from respirometer measurements suggests that the relative rates of respiration at the 3 sites are accurate.

The differences in trends observed when respiration was expressed on a mass basis compared with those on an areal basis demonstrate the necessity of determining the mass of respiring material. Since long-term depression of decomposition activity hence respiration rates will lead to greater accumulation of litter in stressed environments (Babich and Stotzky 1982), relative respiration rates on an areal basis could give misleading results. Determination of the mass of actual material for which respiration was measured (ie. under the chambers) is preferable as it allows for statistical analysis of differences in respiration rates. Coefficients of variation indicated that the sample size of 10 was adequate for measuring in situ and basal respiration rates.

The average rates of CO_2 evolution from the forest floor at the control site are similar to others reported from cool temperate coniferous forests (Table 7), except for those from Alaska.

Mass Loss

The lower rates of mass loss and respiration of needles at the most polluted site indicate a reduction in decomposition activity in response to elevated levels of sulphur dioxide. This is similar to Dodd and Lauenroth's (1981) report of slower decomposition of western wheatgrass in SO_2-fumigated

Table 7: Forest floor respiration rates in some cool temperate coniferous forests.

Species	Location	Respiration Rate[1] mg CO_2 m^{-2} hr^{-1}	Measurement period [2]	Reference
Pinus contorta X banksiana	Alberta, Canada	80 - 180	May - Oct (24 hr)	This study (site 3)
Pinus echinata	Tennessee, USA	156 - 183	Mar - Mar (2 hr)	Witkamp (1966)
Pinus sp	Germany	255	maximum rates	Walter and Haber (1957)[3]
Picea sp	Germany	228	maximum rates	Walter and Haber (1957)[3]
Abies sp	Germany	431	maximum rates	Walter and Haber (1957)[3]
Abies balsamae	Quebec, Canada	65 - 81	July (12 hr)	Lieth and Ouellette (1962)
Pseudotsuga menziesii	Washington, USA	50 - 258	Aug - Aug (24 hr)	Vogt et al. (1980)
Tsuga heterophylla	Washington, USA	108 - 421	Aug - Aug (24 hr)	Vogt et al. (1980)
Abies amabilis	Washington, USA	75 - 385	Aug - Aug (24 hr)	Vogt et al. (1980)
Picea mariana	Alaska, USA	3 - 30	June - Sept (2 hr)	Cowling and MacLean (1981)

1 *by alkali absorption*
2 *months (hours)*
3 *from Singh and Gupta (1977)*

plots relative to non-fumigated controls. It is also comparable to reports of reduced decomposition rates in forests experimentally acidified with sulphuric acid (Baath et al. 1980, Hagvar and Kjondal 1981).

Several investigators have used the litterbag exchange technique to deduce the relative importance of substrate and site factors affecting decomposition activity. Very slight differences in decomposition rates of polluted and unpolluted litter decomposed at non-polluted sites have been observed in response to SO_2 fumigation (Dodd and Lauenroth 1981) or emissions from a metal smelter (Freedman and Hutchinson 1980b) or coking plant (Killham and Wainwright 1981). Although the latter authors attributed most of the observed suppression to particulate deposits on the leaf surfaces, a small difference was still evident when the deposits were removed. Although these differences have usually been found to be insignificant, they seem very consistent, and may indicate a small effect of substrate quality on decomposition in polluted areas.

The placement of unpolluted litter in a polluted environment has usually led to more dramatic alterations in decomposition activity. Significantly reduced decomposition rates have been reported in response to acidification of unpolluted litter (Hagvar and Kjondal 1981, Hovland et al. 1980) or humus (Hagvar and Abrahamsen 1980), or placement of unpolluted

litter at sites previously exposed to "acid rain" (Baath et al. 1980), and increased rates have also been reported (Lee and Weber 1983, Roberts et al. 1980). These studies suggest that the physical, chemical or biological characteristics of the environment in which the litter is decomposed is instrumental in altering decomposition rates.

Results of this study suggest that substrate quality is important in determining decomposition rates during the first few months of decomposition, as respiration of undecomposed needles was significantly lower in site 1 needles, and mass loss over the first summer was significantly lower in needles from site 1 regardless of site of placement. Chemical quality of litter is different at the 3 sites, with higher concentrations of $SO_4^{=}$, Ca, Al and Mn, and lower concentrations of P, Fe, K, Mg, N, and Zn in foliage at sites near the gas plant (Legge 1980). The greater respiration rates after 5, 12 and 17 months, and the greater mass loss during the second summer of needles decomposed at site 3 regardless of site of origin, indicate a prevalence of environmental (site) factors in determining decomposition rates at this time. The improvement in decomposition rates of 1 at 3 needles after the first 5 months may be the result of enhanced substrate quality due to leaching of sulphur deposits or excess sulphate from these needles. The decline in decomposition rates of 3 at 1 needles after this time may be the

result of their aquiring sulphur from the atmosphere or from the surrounding litter. Thus, differences in the chemical nature of polluted and "unpolluted" litter may influence decomposition in the early stages, after which time the nature of the litter environment, especially the degree of sulphur input from the atmosphere or surrounding litter becomes more important.

This relationship between litter source and decomposition rates over the first few months may also indicate a lag phase, before colonization speeds up decomposition of 1 at 3 needles, and before the organisms on 3 at 1 needles are affected by the higher sulphur levels. A sufficiently long lag phase could result in decomposition rates after 5 months bearing a greater relation to site of origin than to site of placement. Chemical analysis of exchanged needles over the first 5 months would help separate effects of changes in substrate quality from those of initial colonization by forest floor organisms, but was not possible in this study.

Higher rates of mass loss of litter in bundles compared with bags have been found by several investigators (Bocock and Gilbert 1957, Witkamp and Olson 1963), and are usually attributed to greater fragmentation loss in bundles, as well as greater intimacy with surrounding litter. The higher variability of data from bundles is probably the result of the sample size being only half as large as that of bags,

as well as the error introduced in correcting for loss of needles. Thus it is probably not a reflection of greater variability in decomposition rates per se, and may not be a general characteristic of the tethering technique. Although bags are believed to enhance decomposition by maintaining higher moisture levels, higher moisture contents in needles from bags were observed on one occasion only, which was the only time at which it had rained within 24 hours of sampling. This suggests that the litterbags may have been retaining moisture and thus may have enhanced decomposition to a small extent. It is unlikely that the bags excluded soil fauna from the needles as a 1 mm mesh is considered large enough to permit passage of fauna present in coniferous forests (Berg et al. 1982). However, as the bags did separate needles from the surrounding litter, they may have impeded colonization by bacteria and fungi during the initial stages of decomposition. As this is also the time during which the moister microclimate in the bags would be most prevalent, it is unlikely that the bags created a significant alteration in decomposition activity. The similar respiration rates of litterbag needles and needles from the surrounding litter (Figures 7 and 6 respectively) suggest that microbial activity in the litterbags was similar to that in the surrounding litter by the time the first bags were removed. Thus, the

results from the litterbags are probably indicative of rates occurring in the litter layer at each of the sites.

The low rates of mass loss observed over the winter differ from the results of other studies which have often indicated this to be a time of rapid decomposition (Hagvar and Kjondal 1981, McBrayer and Cromack 1980, Lousier and Parkinson 1976). As this loss is usually attributed to leaching in response to melting of snow, the low rates observed may be due to the small amount of leachable material in coniferous needles (2% in these needles - B.R. Taylor, personal communication). It may also be that this system is more moisture and temperature stressed in the winter, or less moisture stressed in the summer than other sites. The similar rates of mass loss over the first and second summers is also unusual as initial loss is usually much more rapid than subsequent losses. This may reflect the low leachability of these needles, the time lag involved in the initial colonization during the first summer, or the better environmental conditions during the second summer when the bags were partially covered with fallen litter. The increased variance in mass with time has also been noted by Fogel and Cromack (1977) who attributed it to increasing effects of different micro-environments. Coefficients of variation indicated that the sample size of 20 was sufficient for measuring mass and respiration of decomposing needles.

Decomposition constants (k) for the control site (0.13) are lower than those reported in forests in the southeast (0.42 - 0.58) and northwest U.S. (0.22 - 0.56) (Edmonds 1980), and are also lower than those from other cool temperate coniferous forests (Table 8). This may be a reflection of the cool, dry climate and poor soil at this site relative to other areas. This rather low decomposition rate is consistent with the low rates of litterfall, turnover and respiration also measured at this site.

Litter Turnover

Differences in rates of litterfall between the 3 sites are adequately explained by differences in the size and density of trees at the sites, since rates were similar on a stand basal area basis. A correlation between stand basal area and litterfall has also been reported by Bray and Gorham (1964) and MacLean and Wein (1978a). Litterfall also correlated with density to some extent in that site 3 had the lowest density and the lowest litterfall. This contrasts with findings of several investigators (Bray and Gorham 1964, Fahey 1983, Moir and Grier 1969) of no discernable relationship between tree density and litterfall once the canopy is closed. However, since 5 of the 15 traps at site 3 were in the open part of the plot, the assumption of closed canopy is not met, and these data do not provide a valid test for effects

Table 8: Annual fractional loss of needles in litterbags in some cool temperate coniferous forests.

Species	Location	k [1]	Study Time (yrs)	Reference
Pinus contorta X banksiana	Alberta, Canada	. 0.13	1.5	This study (site 3)
Pinus banksiana	New Brunswick, Canada	0.31-0.36 0.23-0.28	1.0 2.0	MacLean and Wein (1978b)
Pinus contorta	Wyoming, USA	0.24-0.26	1.8	Fahey (1983)
Pinus strobus	Ontario, Canada	0.37-0.50	2.3	Freedman and Hutchinson (1980a)
Pinus jeffreyi	Nevada, USA	0.11	1.0	Stark (1973) [2]
Pinus sp.	Finland (south)	0.43 0.29	1.0 3.0	Mikola (1960)
Pinus sp.	Finland (north)	0.31 0.19	1.0 3.0	Mikola (1960)
Pinus sp.	Finland	0.36	1 summer	Karenlampi (1971) [3]
Pinus sylvestris	Sweden	0.25	2.0	Baath et al. (1980)
Pinus sylvestris	Sweden	0.28-0.31	1 - 5	Berg et al. (1982)
Pinus desiflora	Japan	0.17-0.27		Ando (1970) [4]
Pinus sylvestris	England	0.13	2.0	Kendrick (1959) [3]
Pinus sylvestris	Wales	0.51	1.0	Hayes (1963)
Abies grandis	Wales	0.51	1.0	Hayes (1963)
Picea sitchensis	Wales	0.51	1.0	Hayes (1963)
Picea mariana	Quebec, Canada	0.17-0.20	2.25	Moore (1984)
Picea glauca	Alaska	0.12	1.0	Piene and Van Cleve (1978)

[1] *provided or calculated from mass loss data using the equation* $X/Xo = e^{-kt}$ *where X = mass remaining at time t, and Xo = original mass (at* t_o*). (Olson 1963)*

[2] *cited by Fogel and Cromack (1977)*
[3] *cited by Singh and Gupta (1977)*
[4] *cited by Piene and Van Cleve (1978)*

of stand density on litterfall rates. Since all traps were in proximity to at least one tree, and no significant differences in annual litterfall mass occurred between traps in the "open" and "closed" areas, it is unlikely that litterfall at site 3 was greatly underestimated because of the lower density. Since forest floor and respiration samples were concentrated in the "closed" area where density (6666 stems ha^{-1}) was intermediate to that at the other 2 sites, these data should not be affected by the differences in density among sites. Although some litterbags were in the open area, most of these had been destroyed before the final sampling time and this did not appear to alter relative rates of mass loss at the sites.

The lower litterfall per cm^2 basal area at site 1 may reflect the considerable thinning which has occurred at this site, probably in response to the greater density of trees. This is also evident in the greater height of dead branches, greater number of dead trees (personal observations), and the larger branch component in the litter layer and litterfall at site 1. The tendency for trees at this site to shed younger needles in response to SO_2 (A. Legge, personal communication) may also be involved. The large needlefall at site 1 in September of 1982 compared to that at other sites may reflect earlier needle shedding, however this was not evident the following year.

According to Bray and Gorham (1964), litterfall patterns in cool temperate gymnosperm forests range from distinctly seasonal to more or less continuous. The variation in seasonal litterfall patterns over the 2 years at these sites probably reflects different climatic conditions. Since temperature and precipitation were similar both autumns, the lower autumn litterfall in 1983 was probably due to the higher litterfall which occurred that spring. As this does not appear to have occurred in 1982, it may have been the result of the unusually low snowpack in 1983 which was about 1/3 as deep and melted a month earlier than that in 1981 (Figures 1 and 2, pages 24 and 26). As precipitation is low in spring in this area, the smaller amount of snowmelt water may have created a moisture deficit, which may promote leaf shedding (Kozlowski 1973). If this scenario is correct, then the 1983 pattern was unusual, and litterfall in this forest usually has one marked peak in autumn. Autumn litterfall peaks have been reported in a variety of pine forests (Fahey 1983, Foster and Gessel 1976, Gresham 1982, Wiegert and Monk 1972, Van Lear and Goebel 1976).

The large proportion (93%) of pine needles in litterfall at the sites is greater than Bray and Gorham's (1964) estimates of 60 - 70% for pines and 77% for gymnosperms in cool temperate regions. This difference was probably caused largely by the littertraps in the present study catching overstory litter

only, thus exaggerating the relative proportions of all tree litter. The lower (82%) needle proportion in the litter layer supports this hypothesis. Considerable variation in this parameter among pines and other cool temperate gymnosperms probably exists.

Values for annual litterfall at the control site (1.1 t ha^{-1}) are lower than the 3.7 t ha^{-1} reported by Bray and Gorham (1964) for cool temperate forests, and are also lower than others from cool temperate pine forests (Table 9). This is probably due primarily to the higher latitude of these sites compared with the others. Although annual litterfall at the sites is also lower than the 2.7 t ha^{-1} predicted for forests at this latitude (Bray and Gorham 1964), this value was probably exaggerated by including European forests which tend to have higher litterfall rates than do North American forests at similar latitudes (Bray and Gorham 1964). Also, since they included data from other species besides pines, and since pines tend to grow on poor sandy soil (Foster and Morrison 1976, Miller et al. 1979) and are less productive on these soils (Perala and Alban 1982), their predictions for annual litterfall are probably overestimated for North American pine forests.

The greater mass and depth of the forest floor with proximity to the gas plant suggests increased litter accumulation in response to SO_2 pollution. Although the most polluted

site also receives greater input of litter than the control site, differences in their respective residence times indicate that differences in litterfall are not solely responsible for differences in litter accumulation. The lower rates of respiration and mass loss at the most polluted sites imply that reduced decomposition rates are also responsible for the greater accumulation of litter. Since all forest floor layers (L, F and H) are greater at the polluted sites, it appears that all stages of decomposition are inhibited. Accumulation of organic matter often occurs in polluted environments, as a consequence of disrupted microbial mineralization processes (Babich and Stotzky 1982). Heightened litter accumulation has been reported in aquatic systems subjected to acidification (Grahn et al. 1974, Hendrey et al. 1976), and in forests exposed to heavy metal pollution (Coughtrey et al. 1979, Freedman and Hutchinson 1980b, Strojan 1978, Tyler 1972).

The decrease in forest floor mass over the growing season is consistent with the higher rates of decay and microbial activity recorded during the summer. Forest floor mass at the control site is lower than that reported in other cool temperate pine forests (Table 9). Since decomposition is also slower at this site, the small accumulation of litter is likely the result of the low litter input (Table 9).

Table 9. Litter input, accumulation and residence times in some cool temperate pine forests.

Species	Location	Age (yrs)	Annual Litterfall[1] (t ha^{-1} yr^{-1})		Forest Floor Mass (t ha^{-1})		t[2] (yrs)	k[2] (yr^{-1})	Reference
P. contorta	Alberta, Canada	40	1.12	(O) tree	10.43	(O)	9.3	0.11	This study (site 3)
X banksiana			1.16	(D) tree	15.51	(D)	13.4	0.08	
P. contorta	Wyoming, USA	70	1.5	(D) tree	17.3	(O)	12.0	0.08	Fahey 1983
P. contorta	Colorado, USA	65	4.9	(D) total	25.4-42.1	(D)	5.2-8.6	0.12-0.19	Moir and Grier 1969
P. banksiana	Ontario, Canada	30	3.4-4.2	(D) total	20.0	(O)	5.0	0.20	Foster and Morrison 1976
P. banksiana	New Brunswick, Canada	29-57	1.5-2.0	(D) total	105-130	(D)	24.0-53.0	0.02-0.04	MacLean and Wein 1978a
P. banksiana	Minnesota, USA	40	5.3-6.2	(O) total	25-33	(O)	5.0	0.21	Perala and Alban 1982
P. resinosa	Minnesota, USA	40	5.5-6.9	(O) total	26-33	(O)	4.0-5.0	0.21	Perala and Alban 1982
P. resinosa	Minnesota, USA	60	3.3	(D) total	15.8	(D)	5.0	0.20	Tappeiner and Alm 1975
P. sylvestris	England	35	9.5	(D) total	36.7	(D)	3.9	0.26	Ovington 1959
P. taeda	North Carolina, USA	32	6.1	(O) total	32.9	(O)	5.4	0.19	Jorgensen et al. 1980
P. taeda	South Carolina, USA	17	4.4	(D) tree	20.8	(D)	4.3	0.23	Van Lear and Goebel 1976
P. echinata	South Carolina, USA	40	4.9	(O)	18.4	(O)	3.7	0.27	Metz 1954

[1] *O = organic mass; D = dry mass; tree = overstory litter only; total = overstory + understory litter*

[2] *t = litter residence time = accumulation/input; k = annual fractional loss = 1/t*

The greater residence times for organic matter at sites near the gas plant indicate a long term suppression of decomposition in response to SO_2 pollution. Although determination of litter input rates is essential if litter accumulation is to be used as an estimate of decomposition rates, there do not appear to be any studies which have measured litter input and accumulation in polluted environments. The 9.3 year residence time for organic matter at the control site is longer than most reported for cool temperate pine forests (Table 9). This is consistent with the lower rates of decomposition in these stands, which probably reflect the higher latitude and poor soil.

In order for the litterfall - accumulation method to provide an accurate estimate of residence times and decomposition rates, a number of conditions must be met. First, accurate estimates of litter inputs and standing crops must be determined. The considerable spatial heterogeneity of both litterfall (Bray and Gorham 1964) and forest floor organic matter (Dwyer and Merriam 1981, Frankland et al. 1963) requires that large numbers of samples be taken. Coefficients of variation for this study indicate that the sample size of 15 was sufficient to estimate total litterfall and forest floor masses, mass of needles in litter layers and litterfall, and mass of L and F layers, however it was not sufficient to estimate mass of non-needle components of litter and

litterfall or mass of humus in these forests. High variability of non-leaf litter has also been reported by Bray and Gorham (1964), Hurd (1971), Rochow (1974) and Sykes and Bunce (1970).

Seasonal fluctuations in forest floor organic mass may also occur (Woods and Raison 1982), necessitating sampling at several times during the year, at least at times of maximum (late autumn) and minimum (late summer) levels. Annual fluctuations in litterfall (Bray and Gorham 1964, Woods and Raison 1982) and possibly forest floor mass necessitate sampling for several years to get accurate estimates. In the present study, forest floor mass did not vary much between the two sampling years, and litterfall from June to December did not change in a consistent manner at all sites over the two study years. Therefore, the estimates may be representative of average levels.

An accurate measure of total litter input is difficult to achieve. Since the littertraps used in the present study caught overstory litter only, actual litterfall mass was underestimated. Traps placed on the litter surface would provide a more accurate estimate of above-ground litter inputs, but would have a higher risk of contamination and disturbance. Turnover rates could also be based on overstory litter only, as in the present study. However, both of these approaches would still exclude below-ground inputs such as roots and root exudates, which can be substantial (Phillipson et

al. 1975, Vogt et al. 1983). Although most estimates using above-ground litter inputs only will underestimate litterfall, most studies to date are of this type, and should be acceptable for comparative purposes provided that the forests (species, age and latitude) are fairly similar. Given the similarity of the three stands in the present study, the residence times should allow for valid comparisons between the sites.

Accurate estimates of forest floor mass are hindered by difficulty in separating organic and mineral layers and incorporation of organic material into the mineral soil. These were not major problems in the present study as the layers were quite distinct. Although depth correlated with mass in this study, this relationship should only be assumed if the relative proportions of each organic layer are similar at all sites, because of the differences in density of the layers. Also, since lower layers have lower organic matter content, organic mass should be determined, unless the relative proportions of each layer are similar at all sites.

Woody litter represents a substantial input of organic matter to the forest floor, however, determination of rates of input and accumulation of this litter is inhibited by the extreme variation in its spatial and temporal distribution (Boddy and Swift 1983, Phillipson 1983, Sollins 1982). Input and accumulation of large pieces of wood were not measured in the present study, but because of their slow decay rates

(Graham and Cromack 1982), incorporation of this input would have increased estimates of residence time.

Another important assumption of the litterfall - accumulation method is that the system be in equilibrium with respect to litter inputs and losses from the forest floor (Olson 1963). According to Bray and Gorham (1964), there is no inherent tendency toward higher or lower litterfall with increasing age once the canopy is closed. Several studies (Bray and Gorham 1964, Foster and Morrison 1976, MacLean and Wein 1978a, Turner and Long 1975) have reported more or less constant rates of litterfall in temperate coniferous forests over 30 years of age. According to Olson (1963), forest floor equilibrium should be reached in 3/k years, which would be about 30 years in these stands. This is similar to Foster and Morrison's (1976) finding of slower accumulation after 30 years of age in jack pine forests in Ontario. Since the stands in the present study were 35-40 years old and did not appear to be increasing in forest floor mass or litterfall rates (at least over the two study years), the assumption of steady state may be valid. As Fahey (1983) states, even if this steady-state assumption is not exactly valid, the residence time is useful for between-stand comparisons of forest floor litter accumulations.

Values for fractional annual turnover measured by the litterfall - accumulation method are slightly lower than those derived from mass loss data (0.11 vs. 0.13). This contrasts with many other studies (Edmonds 1979, Lousier and Parkinson 1976, Vogt et al. 1983) which reported estimates from mass loss rates considerably higher than those from litter input-accumulation ratios. These differences have been attributed to: 1) litterbag studies estimating loss rates only for the first few years when loss rates are often highest (Edmonds 1979), 2) invalid assumption of exponential decay (Minderman 1968), 3) exclusion of slowly-decaying woody litter from litterbag studies (Edmonds 1979), 4) underestimation of total litter inputs (Vogt et al. 1983, and 5) invalid assumption of forest floor steady-state (Edmonds 1979). These factors may have been offset in the present study as a result of the low leachability of the needles (2%), and their predominance in the litter. This close agreement in loss estimates supports the assumptions of steady state and exponential decay.

Synthesis

The consistent increases in rates of respiration, mass loss and turnover of litter with distance from the gas plant indicate reduced decomposition activity of forest floors near the sulphur emission source. Given the ecological simi-

larity of the 3 sites in all factors except those attributable to the different sulphur loadings (soil and foliar chemistry), and the consistent correlation between decomposition rates and distance from the gas plant, it is reasonable to conclude that this suppression of decomposition activity is a consequence of the long-term input of sulphur to the forest floor at sites near the plant.

These findings correlate with other reports of lower bacterial numbers (Bewley and Parkinson 1984), reduced microbial biomass, and diminished rates of decomposition of glucose, vanillin, urea and cellulose in organic layers of the forest floor at site 1 (Bewley and Parkinson in prep.). Together, these observations demonstrate a significant disruption of the microbial decomposer community at the site nearest the gas plant. Although populations or activities of soil invertebrates were not analyzed in this study, other investigators have found them to be altered in acidified systems (as discussed earlier), and thus they may also have contributed to the observed differences in rates of decomposition among sites.

The lower rate of decomposition at site 1 may be related to differences in pH, as the pH of organic layers at site 1 (3.5) was significantly lower than that at sites 2 (4.7) and 3 (4.8) (Bewley and Parkinson 1984). Reduced respiration and decomposition at pH levels around 3.5 have been reported by several authors (Baath et al. 1979, Bewley and Stotzky

1983, Chang and Alexander 1981, Strayer and Alexander 1981, Tamm et al. 1977). pH levels below 5.5 inhibit the growth of many species of bacteria and actinomycetes (Gray and Williams 1971), as a result of the hydronium ion concentration itself, or the associated alterations in concentrations of other elements (Alexander 1980). Altered concentrations of many elements have been detected in soil and litter from site 1 relative to the other sites (Legge unpublished), and may be partially responsible for the diminished microbial activity at this site.

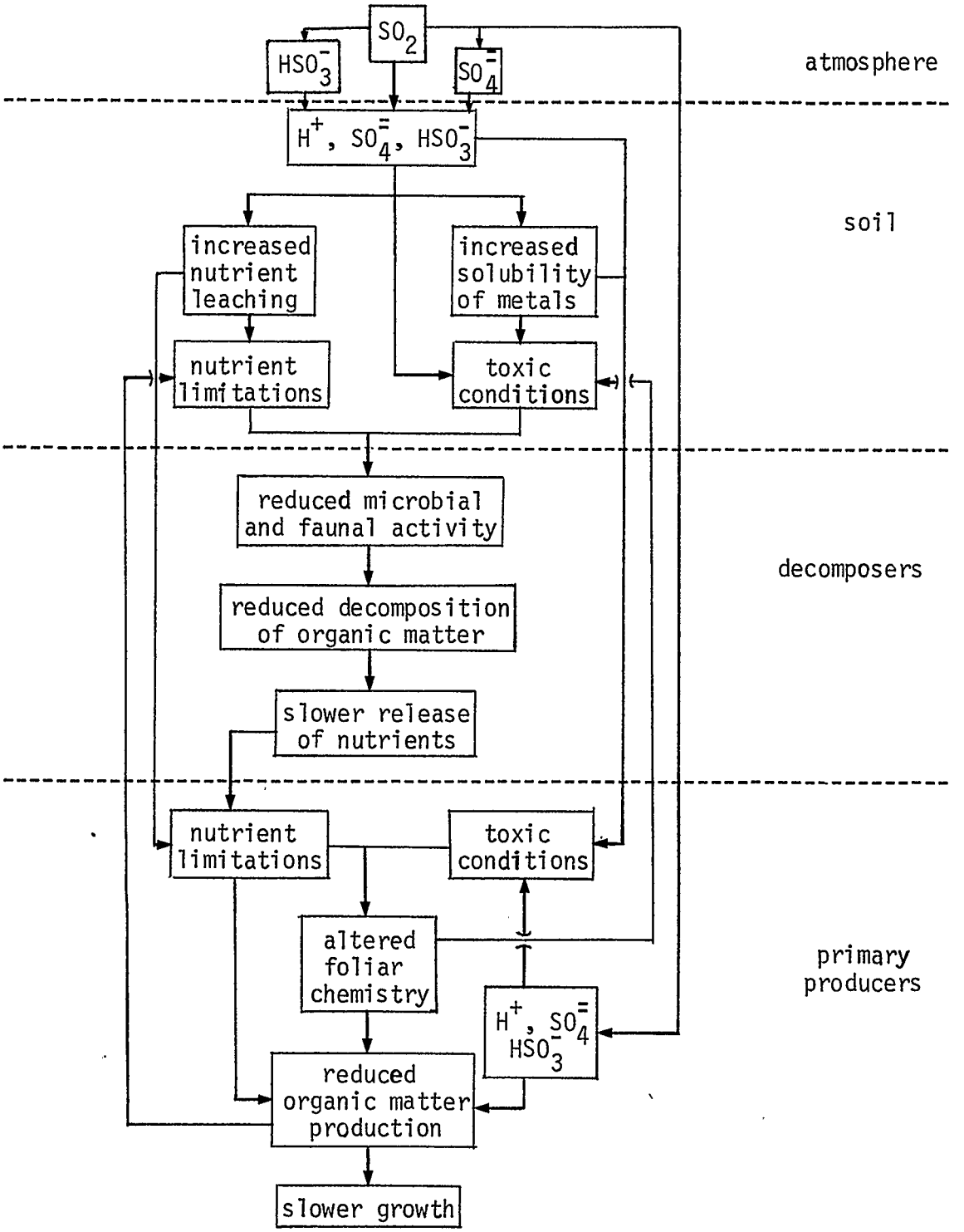
Soil and litter from site 1 also had much higher levels of sulphur (total and sulphate) compared with sites 2 and 3 (Legge unpublished), which may also have limited microbial activity at this site. Sulphur dioxide derivatives (sulphite and especially bisulphite) are known to be toxic to micro-organisms, especially at low pH levels (Babich and Stotzky 1978, Grant et al. 1979). Higher proportions of sulphite and bisulphite-tolerant fungi have been detected at site 1 (Bewley and Parkinson 1984), indicating differential selection in response to high levels of these sulphur compounds at this site.

The altered mineral status of pine needles at site 1 (Legge 1980) may have rendered them less palatable to decomposer organisms, leading to reduced decomposition rates at this site. However, results of the litter exchange experi-

ment suggest that altered substrate quality had a relatively small effect on decomposition rates.

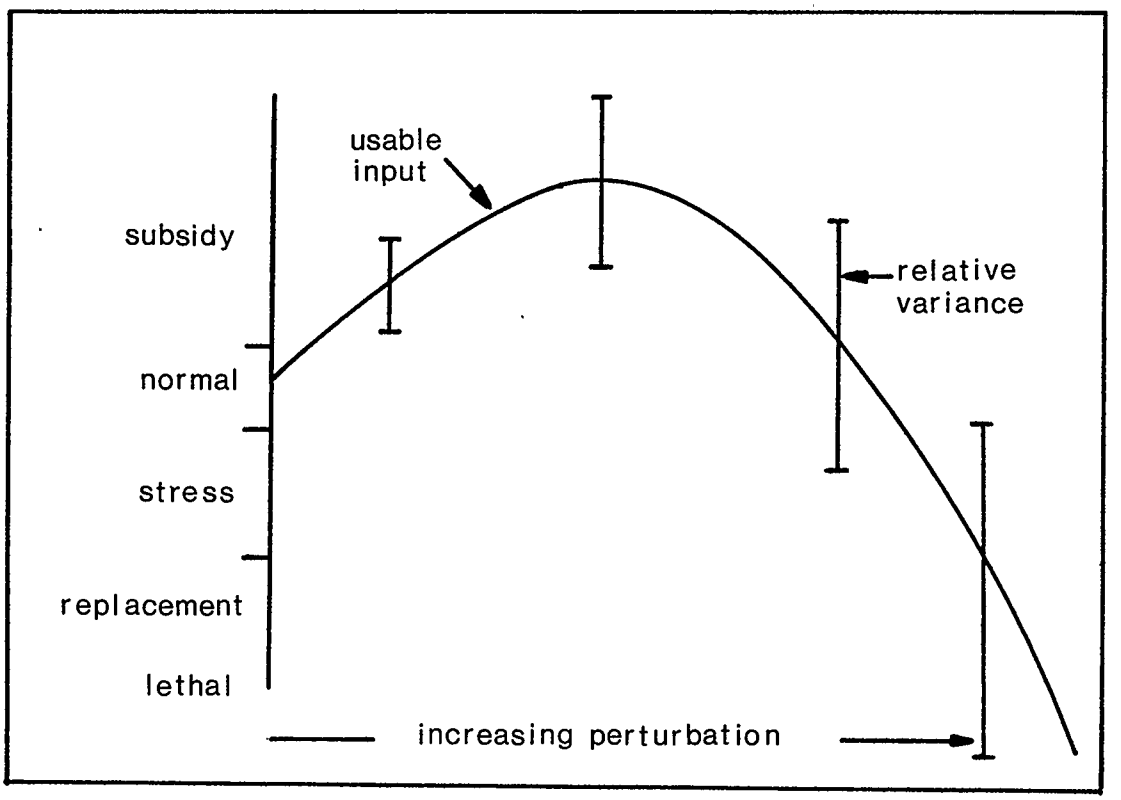
The major relationships between soil chemistry, decomposition and primary productivity in an SO_2-impacted terrestrial ecosystem are outlined in Figure 12. Lower rates of photosynthesis and growth have been measured in pine trees at sites near the gas plant (Legge et al. 1978). This has been proposed to be largely the result of their altered mineral status, which in turn was due largely to SO_2-induced alterations in soil chemistry as well as direct uptake of SO_2 (Legge et al. 1978). Although greater leaching of nutrients and solubilization of metals in response to increased soil acidity may be largely responsible for the altered foliar chemistry, the slower decomposition rates may also be involved as this would also limit nutrient availability in the soil (Figure 12). While increased leaching and solubilization would commence soon after the onset of pollution, the slower release of nutrients from decomposing litter would become increasingly important over time in limiting nutrient availability hence primary production. Given the naturally poor nutrient status of soils at these sites and the number of years (20) that they have been polluted, the slower decomposition rates may be an important factor in the lower primary productivity at sites near the gas plant.

Figure 12. Major pathways in the disruption of mineral element cycling by sulphur dioxide.



"Perturbation" has been defined in ecological terms as "any deviation or displacement from the normal state of structure or function at any level of organization" (Odum et al. 1974). "Stress" refers to any unfavourable deflection where performance of the system is impaired (Odum et al. 1974). Depending on the level of input, pollution by a nutrient such as sulphur may have negligible, "subsidy", "stress", "replacement" or "lethal" effects on the receiving ecosystem (Figure 13). In the present study both structure (microbial biomass and species composition) and function (primary production and decomposition) have been disrupted in an unfavourable manner at the site receiving the most SO_2. Thus it would appear that this perturbation is having a "stress" effect on this forest ecosystem. The effect might be in the "replacement" range as some alterations in relative abundances of groups of micro-organisms appear to have occurred at the most polluted site (Bewley and Parkinson 1984). The absence of alterations in species composition of vegetation at the sites may reflect the extremely low natural diversity of vegetation in this ecosystem. Effects of SO_2 on this forest ecosystem appear to fall into a Class II relationship (subtle deleterious effects which require careful monitoring to detect) of Smith (1974, 1980), as most of the characteristic symptoms (reduced decomposition, photosynthesis, productivity and biomass) have been reported. Although no pathogenic

Figure 13 : Hypothetical performance curve for a perturbed ecosystem subjected to input of a nutrient such as sulphur. The curve simulates the output response (as measured by appropriate systems or component rates of function) to increasing intensity of input perturbation. Adapted from Odum et al. (1974).



outbreaks have been recorded, the trees may be more susceptible to such additional stresses. Lower resistance to pathogens (Shriner and Cowling 1980), insect pests (Smith 1980), drought (Huttunen et al. 1981), cold (Baker et al. 1982), and frost (Davison and Bailey 1982) have been reported in vegetation exposed to SO_2, and have been proposed to be involved in the widespread forest damage occurring in acid precipitation impacted areas of Europe and North America (Wetstone and Foster 1983).

Increased susceptibility to stress might indicate that the system is less stable (i.e. less able to resist changes in the dynamic equilibrium state existing among its structural and functional components - Ricklefs 1979). However, the subtle damage evident at sites near the gas plant suggest that the stress has not been sufficient to shift the ecosystem's "equilibrium" to the degree that recovery (i.e. change to the state which the ecosystem would be in if it was not being stressed) would not be possible in time if the stress was removed (Legge 1980).

The potential for pollutants to disrupt the structure and function of ecosystems necessitates monitoring of these inputs and their ecological effects. Current strategies include monitoring of contaminant transport and fate, biological and natural resource indicators, and ecological effects (Ausmus 1982). Ecological monitoring determines the net

response of biotic and abiotic interactions to the pollutant input, and may be measured at the population, community or ecosystem level (Ausmus 1982). Since ecosystem processes such as productivity, carbon metabolism and nutrient cycling reflect the highest order of biotic-abiotic interactions, they may be affected by changes in any component, and thus may be very sensitive to impacts (Ausmus 1982). Alterations in these processes may precede those at other levels, thereby allowing detection of the stress before it is manifested in a more apparent manner.

As a vital link in nutrient cycles of ecosystems, the decomposition of organic matter is an important process to monitor, preferably in conjunction with measurement of other nutrient fluxes and pools. Decomposition has been found to be affected by a number of pollutants in addition to acidity, including heavy metals (Freedman and Hutchinson 1980b, Ruhling and Tyler 1973, Strojan 1978) and pesticides (Barrett 1968, Gaur and Misra 1977, Ward and Wilson 1973), and thus may be a sensitive indicator of pollution stress.

The three methods used to measure decomposition rates in the present study proved practical and sufficiently sensitive to detect difference resulting from subtle SO_2 pollution. CO_2 efflux has been recommended as a useful parameter of ecosystem function (Reiners 1968) as it integrates the physiological processes of all living components as well as the

physical-chemical interactions in the soil (Van Voris et al. 1980). If sufficient care is taken to reduce effects of non-decomposition sources of CO_2, respiration measurements can provide accurate estimates of actual and potential decomposition rates at the time of sampling. Rates of mass loss provide a more integrated measure of decomposition for the first few years, but are of limited value thereafter. Measurement of litter turnover rates will enable one to determine long-term decomposition rates, but are less accurate in terms of present rates. Since these methods measure decomposition rates over different time periods, they together provide an integrated measure of past and present decomposition rates. The use of more than one method for measuring decomposition has been suggested by other authors (Ausmus 1973, Woods and Raison 1983) in order to overcome the high variability of decomposition rates over time and the inherent inaccuracies in each of the methods.

Two basic types of studies are commonly used to determine impacts of pollutants on ecosystems and their components. Investigations into the effects of short-term (weeks or months) pollution input usually involve artificial application of unrealistically high pollutant doses to sample systems. These studies are useful for determining whether or not the pollutant has the potential to affect the system, process or organism in question. However, the extrapolation of results

from such experiments for predicting effects of more realistic pollution inputs on natural ecosystems is tenuous. Studies of long-term (several years) pollution impact on natural ecosystems are more directly applicable to actual pollution situations, but require more time and allow for less control of extraneous variables. These additional variables may be alleviated to some extent as in the present study by selecting sites which are ecologically analagous.

To date, most studies examining effects of sulphur pollution on decomposition processes have involved short-term application of high concentrations of sulphuric acid to soil or litter samples. Although these experiments have demonstrated that high levels of acid may alter decomposition rates, the mechanisms and effects of such treatments will not parallel those which occur under actual pollution situations. Many of the pathways of effects illustrated in Figure 12 (page 91) would not occur under these short-term, artificial conditions. This difference is evident in the variety of effects resulting from short-term acid-treatment experiments. Depending on the pollutant dose and the sensitivity of the soil or litter used, the application of a nutrient such as sulphur could have either subsidy or stress effects (Figure 13, page 93) over the short term. In contrast, studies involving application of sulphur (as SO_2 or H_2SO_4) for several years (Baath et al. 1979, 1980, Dodd and Lauenroth 1978,

this study) have consistently demonstrated inhibited decomposition with higher sulphur input.

The major factor precluding definitive determination of the effects of acid precipitation on terrestrial ecosystems is the difficulty of relating source to impact. Effects of point-source pollutants, such as SO_2 from gas plants, may be effectively determined by comparing systems at different distances hence pollution loadings, from the source. This method has been used extensively and provides convincing evidence regarding sources and effects of pollutants (Hirsch 1980). Effects of non-point-source pollutants such as acid precipitation which is transported considerable distances before being deposited, cannot be examined in this manner. One can measure changes occurring at a single site over time (Hirsch 1980), however, this requires considerable foresight and involves innumerable confounding variables. Studies monitoring changes over time have provided convincing evidence for atmospheric pollution-induced alterations in precipitation chemistry (Likens et al. 1972, Oden 1968) and aquatic ecosystems (Henriksen 1980, Schofield 1976), but have yet to demonstrate a definitive link between acid precipitation and terrestrial ecosystem productivity (Cowling and Linthurst 1981, Johnson et al. 1981). However, evidence from various forms of monitoring studies have demonstrated that:

1. applications of high concentrations of sulphur (as SO_2, elemental sulphur or sulphuric acid) have the potential to reduce rates of organic matter decomposition, and
2. decomposition has been reduced in natural systems exposed to low or moderate levels of sulphur dioxide or sulphuric acid for several years.

Together, these findings demonstrate a potential reduction in decomposition activity in areas subjected to sulphur deposition. Although the net effect of such pollution on forest productivity will depend on a number of site-specific factors such as nutrient status and the intensity and duration of pollutant input (Johnson et al. 1982), a pollution-induced disruption of decomposition processes could be manifested in reduced productivity of forests, and may be involved in the extensive forest damage currently being reported in industrialized regions of the world.

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APPENDIX I

Scientific and Common Names of Trees Mentioned in the Text

Scientific Name	Common Name
Abies amabilis	Pacific silver fir
Abies balsamae	balsam fir
Abies grandis	grand fir
Picea glauca	white spruce
Picea mariana	black spruce
Picea sitchensis	Sitka spruce
Pinus banksiana	jack pine
Pinus contorta	lodgepole pine
Pinus desiflora	Japanese red pine
Pinus echinata	shortleaf pine
Pinus jeffreyi	Jeffrey pine
Pinus nigra	black pine
Pinus resinosa	red pine
Pinus strobus	white pine
Pinus sylvestris	Scot's pine
Pinus taeda	loblolly pine
Pseudotsuga menziesii	Douglas fir
Tsuga heterophylla	western hemlock

(Smith 1980)