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Botanical Aspects of Acidic Precipitation

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Abstract

Acidic precipitation can be characterized as wet or frozen atmospheric deposition with a hydrogen ion concentration greater than $2.5 \mu\text{eq liter}^{-1}$. Acidic precipitation is perceived as a significant air pollution problem derived chiefly from combustion of fossil fuels, smelting of sulfide metals, and other industrial processes. Precipitation data from the northeastern United States show a mean pH of between 4.0 and 4.2 with a range of from 3.0 to 6.0 among individual events. Although visible injury to plant foliage has been documented in a variety of studies only one case of visible foliar injury from the acidity in ambient rainfalls has been documented. Acidic precipitation can contribute nutrients to vegetation and could also influence nutrient leaching rates from vegetation. Although these processes occur, there are no data that show changes in nutrient levels in foliage that relate to crop or natural ecosystem productivity. Although no consistent patterns are presently known, acidic precipitation may affect host-plant pathogen interactions. Few experiments with field-grown crops or vegetation under natural conditions have been performed. Many of the studies are inadequate because they have been conducted with inadequate replication of treatments coupled with vigorous statistical analyses. Studies with field-grown crops are evaluated. Acidification of fresh waters of the northeastern United States is caused by acid deposition. Such regions in which this acidification occurs have in common, volume weighted mean H^+ concentrations of $25 \mu\text{eq liter}^{-1}$ or higher and slow weathering of granitic or Precambrian bedrock with thin soils deficient in minerals that provide buffering capacity. As freshwater acidification occurs, many plants, invertebrates, and vertebrates are progressively eliminated. Generally, fisheries are severely impacted when lake pH falls below 5.0. Fish are almost always eliminated when the lake pH is below 4.8.

Resumé

La précipitation atmosphérique acide a comme caractéristique que la concentration d'ions hydrogène dans son contenu liquide ou solide est de plus de $2,5 \mu\text{eq litre}^{-1}$ précipitation acide contribue en grande mesure aux problèmes de la pollution de l'air. Elle provient principalement de la combustion de carburants, de la fonte de sulfures et d'autres procédés industriels. Dans le nord-est des Etats-Unis, d'après les données, le pH moyen varie entre 4,0 et 4,2. Dans des cas séparés il va de 3,0 à 6,0. Dans

plusieurs études ont a déterminé que des dommages visibles se font au feuillage, mais ce n'est que dans un seul cas que la documentation est suffisante pour attribuer les dommages visibles à l'acidité de la pluie de cette région. La précipitation acide peut fournir des éléments nutritifs à la végétation et pourrait aussi influencer le taux de filtrage des éléments nutritifs de la végétation. Bien que nous sachions que ces processus ont lieu, il n'y a pas de données, se rapportant à la productivité de la culture agricole ou celle du système écologique naturel, qui nous montrent des changements dans le niveau nutritif des feuilles. La précipitation acide peut avoir de l'influence sur l'interaction pathogène des plantes affectées, mais, jusqu'à présent, on n'en a pas trouvé de manifestations uniformes. Peu d'expériences scientifiques sur la végétation ont été faites dans les champs où dans son habitat. Plusieurs études sont inadéquates: elles ont été faites sans reproduire adéquatement les traitements et sans analyses statistiques solides. Suit une évaluation d'études faites sur des cultures dans les champs. L'acidification des eaux douces dans le nord-est des Etats-Unis est causée par des dépôts acides. Les régions affectées ont toutes une concentration poids/volume moyenne de H^+ de $25 \mu\text{eq litre}^{-1}$ ou davantage. Là où la couche du sol est mince et ne contient pas de minéraux qui puissent servir de tampon, la désagrégation lente des roches de fond granitiques ou précambiennes suit. L'acidification des eaux douces produit la disparition de beaucoup de plantes et d'animaux invertébrés et vertébrés. La pêche est sévèrement atteinte quand le pH des lacs tombe sous 5,0. Il ne reste plus de poisson quand le pH descend sous 4,8.

I. Introduction

Acidic precipitation, wet or frozen precipitation with a H^+ concentration greater than $2.5 \mu\text{eq liter}^{-1}$ (equivalent to a pH of about 5.6) is a significant air pollution problem in North America and Europe. The northeastern portion of the United States is at the center of the high acid rainfall area in North America (Evans et al., 1981a). The high H^+ concentration of precipitation (rain, snow, fog, sleet, and mist) in the northeastern United States is explained by the presence of strong acids. Sulfuric acid contributes a portion of the acidity (Likens et al., 1972; Nørdo, 1976; Oden, 1976) and nitrate and chloride are significant anion components of the total acidity in precipitation (Jacobson et al., 1976; Yue et al., 1976). A significant amount of sulfur dioxide emitted into the atmosphere is converted into sulfuric acid and various ammonium sulfate aerosols (Altshuller, 1976). Particulate sulfur compounds and sulfur oxides may be incorporated into precipitation with conversion to H_2SO_4 (Likens et al., 1972). About 90% of the sulfur in the atmosphere of the northeastern United States is contributed by anthropogenic sources (Galloway and Whelpdale,

1980). A budget estimate for nitrogen inputs into the atmosphere of the Adirondack Mountain Region indicates that 34% of the anions in rain could be attributed to nitrates (Stensland, 1983). Acidic precipitation is only a portion of the total acidity brought to the earth's surface from the atmosphere. Dry fall plus acidic precipitation is termed acidic deposition. The purpose of this paper is to describe characteristics of ambient precipitation and to review and evaluate the impacts that acidity in precipitation has or may have on vegetation. The effects of other biotic or abiotic agents will not be considered unless they have a demonstrated interaction with the effects of precipitation acidity.

II. Characteristics of Atmospheric Deposition

The chemical composition of rainfall in various geographic regions has been determined (Galloway and Likens, 1976; Likens et al., 1976; Semb, 1976). Moreover, various estimates of amounts of SO_2 and sulfate deposited on terrestrial ecosystems have been made. One estimate is that 200 teragrams (tg; 1 tg = 10^{12} g) of sulfur move from the earth's surface to the atmosphere and back again annually (Kellogg et al., 1972). About 15 tg are absorbed by vegetation directly as SO_2 , while about 20 tg (10%) and 80 tg (40%) are deposited as sulfates on terrestrial ecosystems by dry and wet deposition, respectively (Kellogg et al., 1972). A similar estimate of annual sulfur deposition was obtained independently (Friend, 1979). Much of this sulfur impacts upon land areas of the Northern Hemisphere. About 93% of all anthropogenic sulfur production occurs in the Northern Hemisphere and about 80% of this total is deposited on land surfaces in that hemisphere (Friend, 1979).

Although dry deposition of sulfur compounds is significant and these compounds may have some phytotoxic effects at high concentrations, about one-half of atmospheric sulfur reaches the earth's surface in precipitation (wet deposition). Indeed, most of this sulfur is in the form of sulfate with associated H^+ and NH_4^+ ions (Nørdo, 1976). Wet deposition may consist of rain, snow, and fog. Although fog may constitute a significant portion of wet deposition in some areas, it usually does not result in large amounts of moisture input to foliage in most areas of the world. There are no estimates of the total amount of acidity deposited as dew or fog on vegetation.

Data from the National Atmospheric Deposition Program (NADP), for 1978 and 1979 show that the median pH of precipitation in portions of New York, Ohio, and Pennsylvania is less than 4.2, while most of the northeastern portion of the United States has a median below pH 4.4 (NADP, 1978 and 1979). The pH levels derived from NADP are in good agreement with data of the MAP3S and EPRI networks (Pack, 1980).

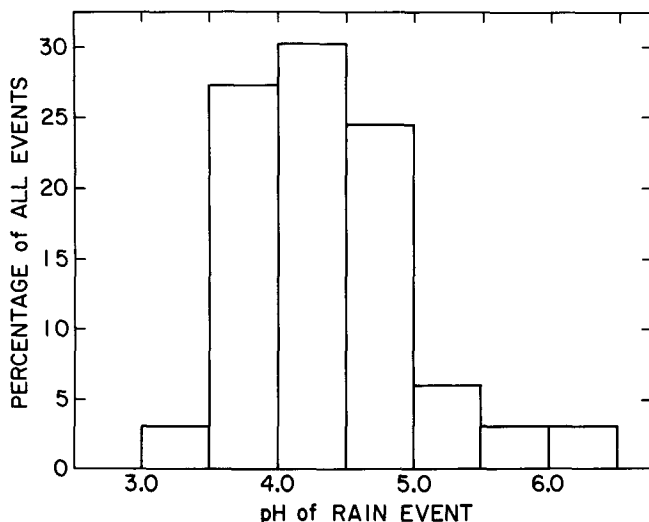


Fig. 1. Frequency distribution of the pH of ambient rain during the 1981 growing season on an event basis at Brookhaven National Laboratory. The figures represent the weighted average of hourly samples collected during each event for the period of 30 May through 29 September 1981. No rainfall events had a mean pH below 3.0 or above 7.0. The volume weighted mean H^+ concentration of all rainfalls was $91.5 \mu\text{eq liter}^{-1}$ (pH 4.04). Data taken from Evans et al. (1983).

Acidity in precipitation events can be categorized by the percentage of rainfalls within various pH ranges. Data of Figure 1 show the frequency distribution of the pH of ambient rainfalls during the 1981 growing season on an event basis at Upton, N.Y. (Evans et al., 1983). The figures represent the weighted volume mean of hourly samples collected with a sequential rain sampler for the period 30 May through 29 September 1981. No rainfall samples had a mean pH below 3.0 or above 7.0. The volume weighted mean H^+ concentration of all rainfalls was $91.5 \mu\text{eq liter}^{-1}$ (pH 4.04). Data from rain samples collected for the years 1976–1979 at MAP3S stations at Ithaca, N.Y.; University Park, Pennsylvania; and Charlottesville, Virginia were chosen to be compared with data from Upton, N.Y. because the former are three representative areas within the northeastern United States (Evans et al., 1981a). Most rainfalls had pH levels between pH 3.5 and 4.5. Thirty-two percent of all rainfall samples had a pH below 4.0. Less than 0.5% of all rainfalls were below pH 3.0 or above pH 5.5. These data demonstrate that a wide diversity in rainfall chemistry is present at several locations and that presenting only long-term (i.e. annual) volume weighted mean pH values may obscure this diversity.

Data from these national or international precipitation chemistry pro-

grams are derived from precipitation collectors that collect wet precipitation over periods of days, weeks, and months. Recent results suggest that most ambient rainfalls during the summer time period of 1982 at an agricultural field site at Brookhaven National Laboratory were of short duration and were of low precipitation rate. Thirty-six events (33% of all events) had durations of less than 2 minutes and 47 events (43%) were shorter than 10 minutes. Forty-two events (38%) were between 11 and 140 minutes while the remaining 19 were longer than 140 minutes. A majority of events had rates less than 1.5 mm hr^{-1} and only 12.5% of all events had rates greater than 3.5 mm hr^{-1} . Over 50% of all ambient showers during the summer period had volumes below 0.25 mm. Moreover, only 8% of all events had amounts greater than 8 mm (Evans et al., 1984a). These data, derived from a rotary rain indicator and a tipping bucket gauge, indicate that the majority of all ambient rainfall events are of relatively short duration and small volume (Evans et al., 1981b; Evans et al., 1982b).

Recently, data were analyzed from other locations in the United States to determine if the frequency and duration of ambient rainfalls were similar to those described above from Long Island. Data from the crop growing seasons (1 May through 30 September) only were analyzed (Evans et al., 1984b) on a minute by minute basis with 0.0042 mm per minute volume resolution. A significant percentage (between 17 and 40%) of all showers recorded at Urbana, Ill., Franklin, N.C., and Seaside Park, N.J., had durations of less than 20 minutes. Similarly, a large percentage had durations of less than 40 minutes (50, 46, and 32% for 3 years at Urbana, Ill., 65% at Coral Gables, Fla., 50% at Franklin, N.C., and 54% at Seaside Park, N.J.). When all data from the six growing seasons were pooled, over 88% of all rainfalls were shorter than 160 minutes (Fig. 2). Similar results were observed when volume measurements were made. Between 38 and 57% of all recorded showers had less than 1 mm at all five stations in the eastern United States. When all data were pooled, over 65% of all rainfalls were less than 3 mm. These data demonstrate that plant foliage is wetted during the growing season by numerous showers which are of short duration and low volume. These data also demonstrate that taking samples over periods of days, weeks, and months to determine rainfall chemical characteristics may obscure a large diversity of characteristics that plant foliage may experience.

These data that document many small-volume, short rainfalls are independent of the frequency and duration of dew on vegetation surfaces. During the 1979 growing season at Upton, N.Y., it was determined that dew conditions were present 65 times for more than 2 hours (a total of 775 hours) (Evans et al., 1981b). Moreover, dew conditions were present 36 times for more than 2 hours (a total of 226 hours) during the 1981

growing season at the same site (Evans et al., 1983). Collectively, these data suggest that foliage is wetted numerous times during the growing season. There is little information about the chemistry of these short-duration, low volume rainfalls as well as dew. The chemistry of these low volume rainfalls and dew is obscured by larger volume precipitation samples in networks that do not sample on an event basis.

Besides the large short term variations in rainfall documented above, large spatial variations also exist. As shown by Evans et al. (1981a), sulfate and nitrate concentrations in rainfall from a single storm near Champaign, Ill. for 2 July 1978 at areas a few kilometers apart varied by a factor of two to three while concentrations of calcium and magnesium varied by a factor of five to six. Moreover, rainfall acidity varied from pH 4.2 to 4.5 over this same area.

Most low pH values in rainwater occur in the spring and summer (Raynor and Hayes, 1978). The mean (weighted) hydrogen ion concentration in rainfalls at Brookhaven National Laboratory was almost 10^{-4} M (pH 4.0) during the summer of 1977. Values for spring were about 0.45 times 10^{-4} M (pH 4.35) and the mean concentrations for winter and fall were similar at about 0.23 times 10^{-4} M (pH 4.64). These observations indicate that acidity of rainfall is highest when most plants are actively growing.

III. Wet Deposition and Foliage

A. INTERACTION OF WATER AND LEAF SURFACES

The amount of injury to plant foliage by acidic precipitation may depend upon the area of leaves in contact with rainwater. Moreover, injury may also depend upon the rate of absorption of materials from rainwater per unit area. The amount of water absorbed by foliage depends upon many characteristics. These characteristics vary among plant species and, as a result, may determine relative species-sensitivity to precipitation acidity.

The amount of foliar injury may be a function of foliar wettability. The attraction of a liquid to a solid surface upon impaction is an important measure of the amount of water retained on the surface. However, the area over which a droplet spreads depends upon the relative amount of attraction between the liquid and the surface. The advancing contact angle has been used as the criterion of leaf surface wettability (Martin and Juniper, 1970) and is defined as the angle between the surface of the leaf and the tangent plane of a water droplet at the circle of contact between air, liquid, and leaf. A zero degree angle would maximize wettability while an angle of 180° would provide virtually no wetting. Contact angles of pure water drops may be as small as 31° on *Phragmites communis* to

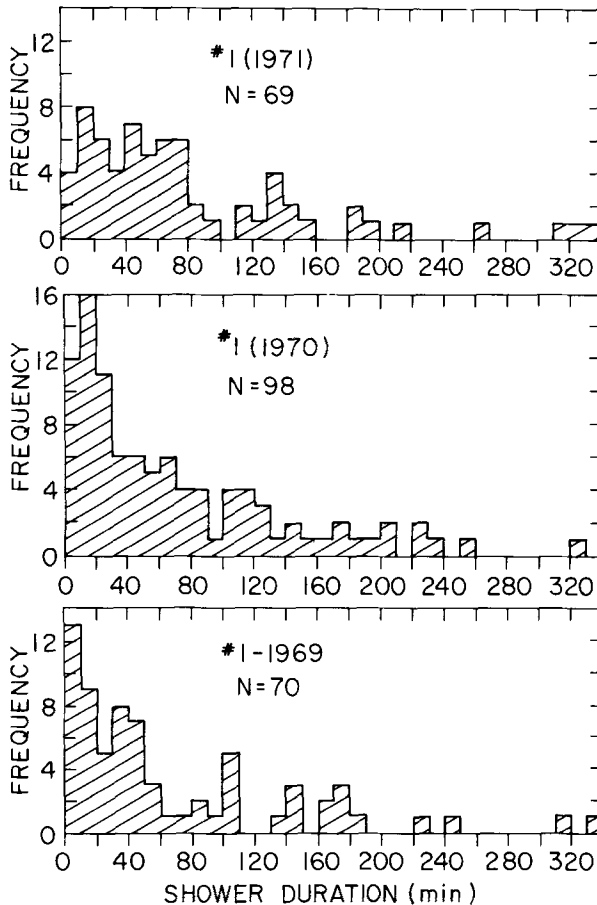


Fig. 2. Frequency distribution of ambient rainfall shower durations (min) for Stations 1 through 4. N values denote the total number of showers per station. For Station 1 (1969) one shower of 1080 min is not shown. For Station 1 (1971) showers of 532 and 567 min are not shown. For Station 2 showers of 510 and 610 min are not shown. For Station 3 showers of 415, 435, and 1238 min are not shown. For Station 4 showers of 437 and 679 min are not shown. Station 1 is Urbana, Ill.; Station 2 is Coral Gables, Fla.; Station 3 is Coweeta Hydrologic Laboratory near Franklin, N.C.; Station 4 is Island Beach State Park near Seaside Park, N.J. Data taken from Evans et al. (1984b).

greater than 150° on *Triticum aestivum* and *Lupinus albus* (Hall et al., 1965; Juniper, 1960; Linskens, 1950). In this way, the contact angle is determined mostly by chemical and physical characteristics of epicuticular waxes and to a lesser extent by surface roughness (Martin and Juniper, 1970). Wettability of leaf surfaces increases markedly when the cuticle and epicuticular waxes are removed (Fogg, 1948).

Solutions must penetrate through cuticle layers or through stomata to reach leaf cells. It has been postulated that cuticles are perforated with micropores (Crafts, 1961). Cuticular pores may be numerous in special-

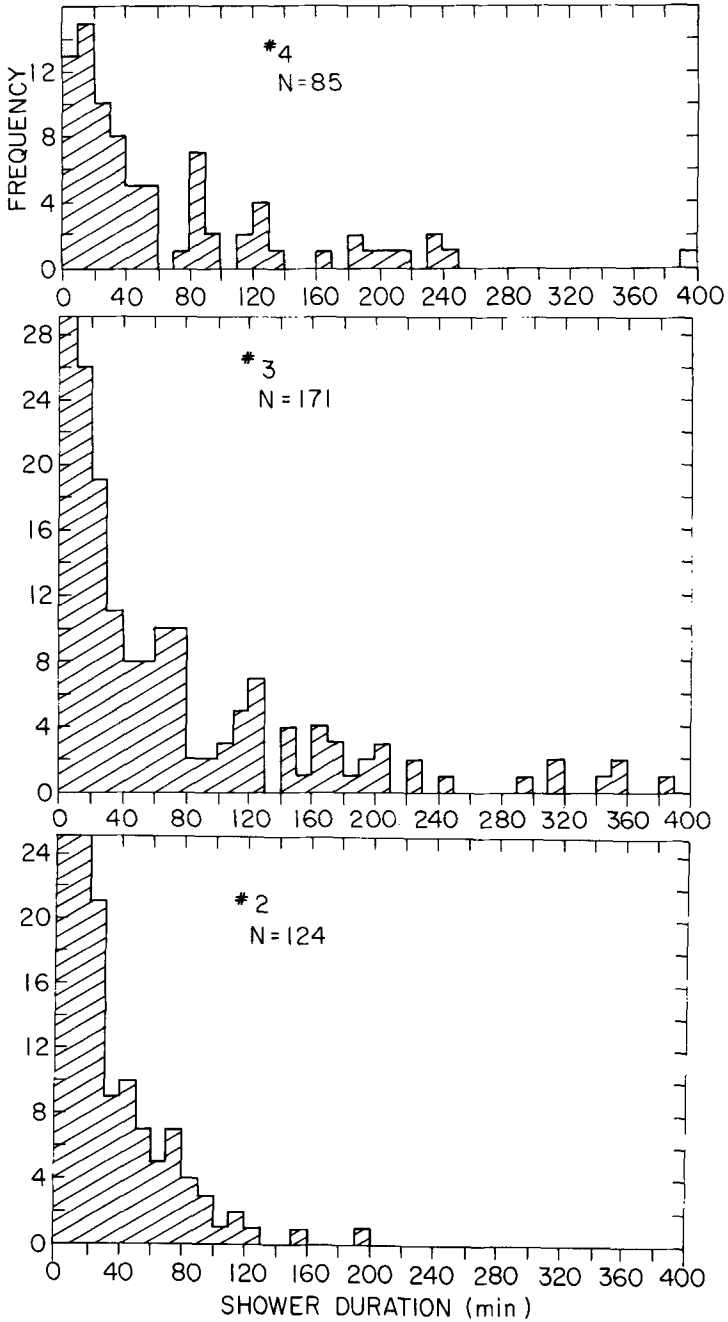


Fig. 2. Continued.

ized areas such as at bases of trichomes, hydathodes, glandular hairs (Schnepf, 1965), water-absorbing scales of Bromeliaceae (Haberlandt, 1914), and stigmas (Konar and Linskens, 1966). Although cuticular pores may not be present (Martin and Juniper, 1970) solutions penetrate faster at these locations. These results may explain why injury from acidic precipitation occurs more frequently at bases of trichomes and hydathodes (see below). Penetration of rain or leaf surface solutions through stomata is thought to be infrequent if it occurs at all (Adam, 1948; Gustafson, 1956, 1957; Sargent and Blackman, 1962). Generally, spontaneous water infiltration of stomata will occur if the contact angle is smaller than the angle of the aperture wall. The degree of stomatal opening from 4 to 10 μm is of little importance in penetration. However, cuticular ledges present at the entrance to the outer vestibule and between the inner vestibule and substomatal chamber resulted in very small wall angles. These small wall angles may not be adequate enough for water penetration of stomata (Schönherr and Bukovac, 1972). All evidence suggests that the main route of entry of substances should be through the cuticle and not through stomata.

Non-polar molecules should penetrate the cuticle at rates faster than those of polar molecules because of the non-polar nature of both cutin and epicuticular waxes of the cuticle (Norman et al., 1950). More polar compounds, such as inorganic ions and water, may preferentially enter the leaf via pectinaceous channels that traverse the cuticle (Roberts et al., 1948). It is postulated that the ratio of cutin to wax in the cuticle greatly influences the degree of penetration of polar substances (Martin and Juniper, 1970).

Solution acidity may also affect cuticular penetration rates (Schönherr, 1976; Schönherr and Schmidt, 1979). In experiments with isolated apricot leaf cuticles, penetration rates of acidic substances increased with an increase in solution acidity. The penetration rate of basic substances increased with a decrease in solution acidity. These relationships between pH and sorption rates with apricot cuticles (Orgell, 1957) have been verified with isolated cuticles (McFarlane and Berry, 1974) and intact bean leaves exposed to buffered solutions (Evans et al., 1981c).

Cuticles and epicuticular waxes should not be considered to be inert, non-differential barriers to ion permeability. Relative permeability coefficients of isolated cuticles to various mono- and divalent cations differ by as much as a factor of six.

The idea of differential or selective uptake of chemical constituents by foliage is reinforced by other experimental data. Penetration of chemicals into foliage is affected by both metabolic and non-metabolic processes. Reversible diffusion through cuticles is followed by metabolically-controlled uptake through cellular membranes (Prasad and Blackman, 1962).

There are many examples of light-enhanced foliar uptake (Bennett and Thomas, 1954; Gustafson, 1956; Sargent and Blackman, 1965) being retarded by protein synthesis inhibitors (Jyung and Wittwer, 1964). In this way, uptake of various elements by foliage is selective to an unknown degree and is dependent upon the metabolism of leaf cells.

Some regions of the cuticle are more permeable than others. For example, basal portions of trichomes and guard cells (Dybing and Currier, 1961; Sargent and Blackman, 1962) are preferential sites of absorption. Moreover, absorption of water-soluble materials may be rapid through the cuticle near veins (Leonard, 1958; Linskens, 1950). These studies are germane because about 95% of all foliar lesions following exposure to simulated acidic rain occur near the bases of trichomes, at guard and subsidiary cells of stomata, and along veins (Evans and Curry, 1979; Evans et al., 1977a, 1977b, 1978). More recently, these results have been confirmed with other species (Adams, 1982; Paparozzi, 1981). From these data it seems reasonable to conclude that phytotoxic components of simulated acidic precipitation penetrate the cuticle at faster rates near vascular tissues, subsidiary cells, and at the bases of trichomes and hydathodes, etc.

Acidic precipitation may change the surface characteristics of foliage. It has been suggested that acidic precipitation may affect the submicroscopic structure of the epicuticular wax layer(s) of leaves. Shriner (1974) presented scanning electron micrographs that showed that leaves of kidney bean and willow oak exposed to simulated rain of pH 3.2, had eroded superficial waxes, cutin, and cuticular waxes. There was only slight erosion on leaves exposed to pH 6.0 rain. In contrast, Paparozzi (1981) used scanning and transmission electron microscopy and showed no erosion of epicuticular or cuticular waxes on either yellow birch or kidney bean after exposure to simulated rainfalls of pH's as low as 2.8. The cuticular waxes were not structurally changed by simulated acidic rain even though underlying cells were affected. Moreover, the most widely used methods of isolating cuticles involve exposure to strong acids (Holloway and Baker, 1968; McFarlane and Berry, 1974). Penetration rates of elements through isolated cuticles were similar to rates through intact cuticles in situ (Evans et al., 1981c). Presently, a relationship between changes in the cuticle, including cutin and epicuticular waxes, and changes in leaf cells remains to be established.

Leaf surfaces may also change the chemistry of rain solutions. The acidity of rainwater may be changed by chemicals from leaves as raindrops dry. Adams (1982) demonstrated that leaves of several plant species have differing buffering capacities. The pH of simulated raindrops (50 μ l) of pH 5.6, 3.5, and 3.0 usually increased during the 75 minute time period of measurements. However, when the initial pH was 2.5 the pH always

decreased as time passed. The pH of a parafilm surface (control) was always lower than that of any of the plant surfaces suggesting that the leaves produced substances to neutralize the acidity. The presence on leaf surfaces of substances produced by leaves has been recognized for almost a century (Uphof, 1962). Recent results from our laboratory (Evans et al., in press) substantiate the results of Adams (1982). However, in our studies the differences between pH changes on bean leaves not exposed to any solutions and teflon plates (controls) were not marked as the differences documented by Adams (1982) although the test solutions were very similar.

B. INPUTS OF MATERIALS INTO FOLIAGE

A wide variety of chemicals are found in ambient rain in the eastern United States (Galloway et al., 1982; Lindberg, 1982; Lindberg et al., 1981; Reuther et al., 1981). We need to know if materials in rain can be absorbed by foliage and if rainfalls can remove materials from foliage. Recent information suggests that materials can be absorbed at differing rates from rainfalls of varying acidity (Evans et al., 1981c). For example, sulfate penetrated leaves faster at pH 2.7 than at 5.7 while $^{86}\text{Rb}^+$ penetrated faster at pH 5.7 than at lower pH levels. Tritiated water entered foliage at similar rates at all pH levels tested. In addition to differences in uptake due to acidity, incorporation rates of various ions may vary markedly. Water penetrated leaves much faster than $^{86}\text{Rb}^+$. In addition, water molecules entered foliage about one thousand times faster than sulfate ions (Evans et al., 1981c). These results suggest that absorption of materials in water on leaf surfaces is a selective process that may be affected by solution acidity, cellular metabolism, and possibly other factors. However, individual ions appear to have their own specific entry which may be affected by many intrinsic and extrinsic factors.

Foliar fertilization may occur by inputs of nitrogen and sulfur from ambient rainfalls. Little information is available to evaluate the amount of incorporation of nutrients in rain into foliage. The rate of entry of sulfate is a low percentage of the amount in solution (Evans et al., 1981c). The only other information about the incorporation of nitrogen and sulfur into foliage from solutions may be derived from foliar fertilization experiments. Of course, the application of fertilizers on foliage is usually performed with surfactants, not present in ambient rain, to enhance uptake.

Increases in soybean seed yields may result if large quantities of N (80 kg ha⁻¹), P (8 kg ha⁻¹), K (24 kg ha⁻¹), and S (4 kg ha⁻¹) are applied to foliage of soybeans during pod filling only (Garcia and Hanway, 1976). From available evidence the optimum NPKS proportions in the fertilizer

solutions for soybeans should be 10:1:3:0.5. Inconsistent results occurred with other combinations so that many other nutrient combinations, even with high nitrogen (24 kg ha^{-1}) and sulfur (12 kg ha^{-1}) applications, resulted in no yield effects (Garcia and Hanway, 1976).

Throughout the soybean season of 1981 at Upton, N.Y., a total of $18.1 \text{ kg N ha}^{-1}$ (as nitrate) and 102 kg S ha^{-1} (as sulfate) were applied in simulated rainfalls at pH 2.7 and no obvious growth stimulation occurred (Evans et al., 1983). These rather high inputs of N and S can be compared to the relatively low (1.80 kg N and 2.73 kg S per hectare) amounts applied by ambient rainfalls during the same time period. There are no experimental data that document enhanced plant growth by foliar fertilization of any plant species at N or S concentrations present in ambient rain.

C. LEACHING OF MATERIALS FROM FOLIAGE

Since plants produce substances on their surfaces, it is of interest to determine if the removal of these substances is sensitive to acidity in precipitation. Likewise, substances within leaves may be released after exposure to rainfalls. Moreover, the nutrient levels in harvested portions of crops may affect the quality of foodstuffs. It is conceivable that precipitation acidity could sufficiently influence nutrient leaching from plant surfaces as to alter crop quality. Wood and Bormann (1975) demonstrated that K^+ , Ca^{2+} , and Mg^{2+} were leached from pinto bean leaves more rapidly at pH levels of 3.0 and 3.3 than at pH levels of 4.0 and 5.0. Calcium ions leached faster at pH 3.0 than at pH 3.3 from foliage of sugar maple. Leaching rates of K^+ and Mg^{2+} were higher at pH 3.0 than at pH 4.0. In tobacco leaves, Ca^{2+} leached faster from foliage exposed to simulated rainfalls of pH 3.0 than from foliage exposed to pH 6.7 (Fairfax and Lepp, 1975). In pinto beans exposed to a 20 minute daily treatment of simulated rain for five days, more calcium, nitrate, and sulfate were leached from foliage at pH levels of 2.7, 2.9, and 3.1 than from plants exposed to pH 5.7 (Evans et al., 1981c). In contrast, the amount of potassium leached was greater from leaves exposed to pH 5.7 than from leaves exposed to pH levels between 3.4 and 2.9. The amounts of ammonium, magnesium, and zinc leached were the same at all pH levels tested. Three radioisotopes were detected from leachates from leaflets of *Phaseolus vulgaris* that were exposed to one 20 minute rainfall 24 hours after radioisotope addition. Although the quantities of $^3\text{H}_2\text{O}$, $^{86}\text{Rb}^+$, $^{35}\text{SO}_4^-$ were less than 1% of the radioisotopes in leaflets, these results demonstrate that recently absorbed ions may be leached by rainfall.

Cole and Johnson (1977) measured pH and conductivity (a measure of the total cations and anions present) of ambient precipitation and throughfall during two rainfalls in 1973. During the latter portion of the first

rainfall, the pH of the throughfall (≈ 4.0) was about one pH unit below that of ambient precipitation (≈ 5.0). Conductivities of the two solutions were similar at about $10 \mu\text{mho cm}^{-1}$. During the second rainfall, the pH of ambient precipitation (≈ 3.5) was almost two units below that of the throughfall (≈ 5.3). Over an entire annual cycle, the amount of sulfur in throughfall was greater than in the ambient precipitation. Cole and Johnson (1977) concluded that the differences in sulfur content observed were due to foliar leaching. Moreover, van Breemen et al. (1982) demonstrated that ammonium, nitrate and sulfate volume-weighted concentrations are higher in throughfall and stemflow than in ambient rain from forests at two locations in the Netherlands. These results would suggest that N and S may be leached from trees when exposed to rainfalls of pH 4.29 and 4.51. However, washoff of dry deposition may have contributed to higher sulfate concentrations in throughfall. Presently, there are no data that document significant foliar leaching of materials at present levels of precipitation acidity that could produce changes in plant growth or productivity.

D. CHARACTERISTICS OF VISIBLE FOLIAR INJURY

Presently, there is only one documented occurrence of visible foliar injury attributed to ambient rainfalls (Evans et al., 1982a). Visible foliar injury, identical to that caused by simulated acidic rainfalls of pH 4.0 and below, was produced on foliage of field-grown garden beets during a three-day period in which three short durations, low volume rain showers with levels of about pH 3.8–3.9 occurred during the 1980 growing season at Brookhaven National Laboratory. Higher acidity simulated rainfalls resulted in lower beet yields. These lower yields resulted from both a smaller number of saleable roots per plot and a lower fresh mass per saleable root.

Presently, almost all of the knowledge about visible foliar injury is derived from exposures of plants to simulated acidic rainfalls. Lesions produced by simulated acidic rain occur mostly on leaves and reproductive structures (Evans and Curry, 1979; Evans et al., 1977b, 1978; Gordon, 1972; Jonsson and Sundberg, 1972). Visible lesions on leaves have not been observed at pH's above 3.9. A significant percentage of the leaf area may exhibit lesions. For example, about 0.5%, 2 to 3%, 5 to 10%, and 10 to 15% of the leaf area of pinto beans is injured after one to four exposures to acidic rain at pH levels of 3.0, 2.7, 2.5, and 2.3, respectively (Evans and Lewin, 1980). In this way, the area showing injury increases with an increase in simulated rainfall acidity.

Visible leaf injury is most pronounced on foliage of some species just prior to full leaf expansion (Evans, 1980, 1982a; Evans and Curry, 1979; Evans et al., 1977b, 1978). Densities of trichomes and stomata per unit

leaf area are highest in young leaves and lowest in fully expanded leaves. Since the amount of visible leaf injury does not coincide with the density of either stomata or trichomes at full leaf expansion, other factors such as surface wettability must be involved in predisposing leaves to injury. Wood and Bormann (1974) suggested that young (14-day-old) birch seedlings are much more sensitive than older (six weeks old) seedlings. Pappozzi (1981) showed that mature birch leaves were as susceptible to foliar injury as enlarging leaves. Needle elongation is inhibited if simulated acidic rain solutions are applied to immature pine fascicles (Gordon, 1972; Hindawi and Ratsch, 1974).

Leaves of several plant species have reacted to exposure to simulated acid precipitation by producing galls that elevated the adaxial leaf surface (Evans et al., 1977b, 1978). Water from subsequent rainfalls did not pool in these elevated locations so less injury (total area) resulted. Galls were produced from abnormal cell proliferation (hyperplasia) and abnormal cell enlargement (hypertrophy). These results have been confirmed on *Artemisia tilesii*, *Phaseolus vulgaris*, and *Spinacia oleracea* (Adams, 1982). In this manner, the hyperplastic and hypertrophic responses of foliage may have alleviated extensive foliar injury and thus may be responsible for species sensitivities to visible foliar injury.

Experiments were performed to rank species sensitivities to simulated acidic rain. Based upon visible effects on foliage it has been suggested that plants rank in sensitivity from high to low in the following order: herbaceous dicots, woody dicots, monocots, and conifers (Evans, 1980; Evans and Curry, 1979). Within each species, the amount of visible leaf injury appears to relate linearly to the hydrogen ion concentration of the simulated rain solution (Evans, 1982).

IV. Effects on Vegetation

A. INFLUENCE ON FOLIAR GAS EXCHANGE

Several years ago it was proposed that acidic precipitation might affect the rate of gas exchange by stomata (Tamm and Cowling, 1977). Epidermal cells may be injured preferentially upon initial exposure to acidic rain (Hanson et al., 1975; Hewitt et al., 1968). Since guard cells are affected preferentially, it was postulated that acidic precipitation might affect gas exchange rates. In *Phaseolus vulgaris* diffusion resistance was much lower in foliage exposed to simulated rain of pH 2.7 and 3.4 compared with foliage exposed to rain of pH 5.7 (Evans et al., 1981c). These results suggest that foliage exposed to acidic rain may be more subject to wilting or water stress. Moreover, such foliage may be more sensitive to exposures of gaseous air pollutants. This decrease in resistance may also increase

photosynthetic CO₂ uptake. Knowledge of the effects of rainfall acidity in combination with gaseous pollutants such as ozone and sulfur dioxide is needed to understand the total impact acidic rain might have on vegetation.

B. INFLUENCE ON CELL METABOLISM

Even though the cell cytoplasm has a large buffering capacity (Thomas et al., 1944), small localizations of protons reacting with membranes could, at least, modify membrane function in terms of the electron or proton gradient pumps necessary for intracellular energy production even if they do not alter membrane permeability and/or integrity. Subtle alterations in membrane function could alter energy relations of cells (Manson et al., 1977). According to the chemiosmotic theory of energy production, a slight change in the proton concentration across a membrane may disrupt the production of ATP by cells (Hinkle and McCarty, 1978). Of course, disruption of the plasmalemma would produce rapid cell necrosis. The actual mechanism(s) by which protons on foliage have phytotoxic effects at the cellular level is (are) unknown.

The metabolic conversions of both sulfate and nitrate (major anions in acidic precipitation) in plants are known in some detail (Hewitt, 1975; Hewitt et al., 1968; Schiff and Hodson, 1973). Both sulfur and nitrogen are essential elements for plant nutrition. Foliar applications of small quantities of sulfate and nitrate might be incorporated into molecules such as proteins that are vital to cells (see above). From available evidence it seems unlikely that current sulfate and nitrate concentrations in ambient rainfalls could be phytotoxic.

Photosynthesis and respiration measurements were made using leaves of *Phaseolus vulgaris* after exposure to simulated acid rain (Ferenbaugh, 1976). Lesions occurred on leaves after exposure to pH levels of 2.0 and 2.5 as compared with pH 5.5. Although photosynthetic and respiratory rates were higher in leaves exposed to acidic solutions than in control leaves, net photosynthetic rates (photosynthesis minus respiration) were similar at all rainfall pH levels tested when results were compared on a fresh weight basis. As a result there was no change in carbohydrate production. However, leaves exposed to simulated acidic rain (pH 2.3) had lower sugar and starch contents as compared with plants exposed to simulated rain of pH 5.7. Foliage exposed to acidic rain may be stressed but short-term measurements of photosynthesis and respiration may not be sensitive enough to detect the stress.

C. SEED GERMINATION AND SEEDLING EMERGENCE

Lee and Weber (1979) exposed seedlings of 11 woody species to simulated rainfalls (23 mm weekly) of pH 3.0, 3.5, 4.0, and 5.6 for up to nine

months. Seedling emergence of eastern white pine (*Pinus strobus* L.), yellow birch (*Betula alleghaniensis* Britton), eastern red cedar (*Juniperus virginiana* L.) and Douglas-fir [*Pseudotsuga menziesii* (Mirbel) Franco var. *menziesii*], was significantly higher during exposure to high acidity rainfalls as compared with controls. In contrast, emergence was lower for staghorn sumac (*Rhus typhina* L.) under acidic rain exposures as compared with controls. No significant treatment effects were detected for seven other species tested. In similar experiments by Raynal et al. (1980) seedling emergence of yellow birch and red maple (*Acer rubrum*) was inhibited at low pH levels as compared with controls, while emergence of white pine was highest after exposure to simulated acidic rain. No significant treatment effects were present for sugar maple (*A. saccharum*). Moreover, Baldwin (1934) found better germination of red spruce (*Picea rubra*) under more acidic conditions. From available data, it seems that seedling germination and emergence can occur over a wide range of substrate pH levels.

At present, it is not possible to evaluate the ecological significance of acidic rain treatment effects as they relate to natural systems. This statement is true because experiments have not been conducted under field conditions in which rainfall acidity is the only variable that could affect productivity.

D. CROP GROWTH AND YIELD (CONTROLLED ENVIRONMENTS)

Reductions in dry weight of trifoliolate leaves and dry weights of pods and seeds of bush beans (19 and 11% respectively) occurred after exposure to acidic mists (pH 3.0) with no visible leaf injury (Hindawi et al., 1977). In contrast, Wood and Bormann (1974) showed that simulated acidic mists of pH 3.0 did not reduce growth rates of yellow birch even though all leaves exhibited some leaf pitting and curling. However, plant productivity (crop yields) and/or individual survival, etc. may be determined by development and survival of reproductive organs as well as by cumulative injuries to foliage. Since no clear view of yield effects has been demonstrated among various plant species exposed to acidic precipitation, a clear relationship between foliar injury and seed yield cannot be predicted with present knowledge.

Lee et al. (1981) conducted experiments with 28 crops grown in pots in field chambers. Simulated acidic rain was applied at pH levels of 5.6, 4.0, 3.5, and 3.0. Marketable yield was inhibited for five crops (radish, beet, carrot, mustard greens, and broccoli) and stimulated for six crops (tomato, green pepper, strawberry, alfalfa, orchard grass, and timothy). No consistent effects were observed for 16 other crops. The experimental results suggest that the probability of yield being affected by acidic rain depends upon the plant species as well as the part of the plant utilized.

Foliar injury was not always related to effects on crop yields. The marked decreases in root yields of greenhouse-grown radish (Lee et al., 1981) were verified by other experiments (Evans et al., 1982b). In contrast, yields of alfalfa, wheat, and lettuce grown under controlled environmental conditions were not markedly affected by applied simulated rainfalls between pH's 5.6 and 3.1 (Evans et al., 1982b).

In recent experiments, simulated acidic rain of pH 3.1 and below decreased dry mass of seeds, leaves, and stems of pinto beans exposed to 45 20-minute rainfalls throughout the growing season under greenhouse conditions (Evans and Lewin, 1980). The decrease in seed yield noted was similar to the decrease in biomass of both leaves and stems. The decrease in yield of pinto beans by simulated acidic rain was attributed to both a decrease in the number of pods per plant and a decrease in the number of seeds per pod. In soybeans, application of 78 simulated acidic rainfalls decreased the dry mass of both stems and leaves. Seed yield also decreased after treatment with rain at pH 2.5. However, an increase in seed yield occurred when plants were exposed to rainfalls of pH 3.1. A larger dry mass per seed was responsible for the larger dry mass of seeds per plant exposed to simulated rainfalls of pH 3.1 (Evans and Lewin, 1980).

Significant effects of rainfall acidity were not observed on apple seedlings unless the pH was below 2.75 as compared with controls (pH 5.6). Moreover, both leaf and seedling growth rates were not different between pH 7.0 and 2.75 when 14 plants per treatment were harvested after nine, once weekly (amount of water applied not given) rainfalls (Forsline et al., 1983a). The pH levels of ambient rainfalls did not affect fruit quality or production in grapes or apples. However, reductions in pollen germination, fruit set, and fruit quality were observed below pH 3.1 for some cultivars (Forsline et al., 1982, 1983b).

E. CROP GROWTH AND YIELDS (FIELD-CONDITIONS)

Because radish root yields were reduced after exposure to simulated acidic rainfalls under controlled conditions (Lee et al., 1981), two experiments have been performed with field-grown radishes (Evans et al., 1982a; Troiano et al., 1982). Troiano et al. (1982) exposed four plots per treatment and demonstrated significantly higher root yields (13% of dry mass) at high acidity rainfalls as compared with simulated rain of pH 5.6. In contrast, no statistically significant yield effects were demonstrated in an experiment that utilized 45 plots per treatment (Evans et al., 1982a). The mass of individual roots harvested in the former experiment (Troiano et al., 1982) was three to four times greater than yields of the latter experiment (Evans et al., 1982a) and from roots purchased from commercial

markets. The results of these two field studies indicate that the response(s) of plants to rainfall acidity under field conditions may differ markedly from that (those) obtained under controlled environmental conditions (see above effects with radishes grown under controlled environmental conditions). The reason(s) for this difference is (are) not known.

Significant reductions in garden beet yields were obtained with plants receiving applications of simulated rainfalls in addition to ambient rainfalls. Plants exposed to simulated rainfalls of pH 2.7, 3.1, and 4.0 gave yields 73, 77, and 65% of the root yields of plants exposed to rainfalls of pH 5.7 (Evans et al., 1982a). No significant yield reductions were obtained for kidney beans and alfalfa.

Several field experiments have been performed with soybeans. In one experiment (Experiment 1) at Yonkers, N.Y., plants were grown in open top chambers (OTC), one treatment per chamber (Jacobson et al., 1980; Troiano et al., 1983). The experimental treatments were simulated rainfalls at pH's 4.0, 3.4, and 2.8. A clear plastic tarpaulin was loosely secured over the top of each chamber. Within the OTC's, light transmission was decreased up to 25% and temperatures were elevated up to 3°C above ambient conditions. Eighteen simulated rainfalls of 12.7 mm each for a duration of 60 minutes were applied over a period of 50 days during the latter portion of the growing season. These simulated rainfalls provided a mean of 4.6 mm of water daily.

A second experiment (Experiment 2) was performed in Kendall County, Ill. in 1977 and 1978 (Irving and Miller, 1981). Experimental plots were placed at two different locations in the same field during the two-year study. Only one experimental plot (four 5 m rows in 1977 and four 6 m rows in 1978) per treatment was used each year. In both years, simulated rain and ambient rain treatment plots were also exposed to both ambient and artificially elevated concentrations of sulfur dioxide. The treatments were pH 5.25, 4.09 (ambient only), and 3.06 (1978; 3.17, 1977). Simulated rainfalls were distributed from a single nozzle for each treatment plot while sulfur dioxide was administered from a gas distribution system above the plant canopy level.

Eight and 11 simulated rainfalls provided 3.38 and 4.46 cm of water in 1977 and 1978, respectively. These treatments provided 36 and 49% more water to the experimental plots than the control plot which received only 9.39 cm of water during the treatment period of 1978. Thus, not all plots received the same amount of water. Plants were exposed to 11 simulated rainfalls 1.4 times weekly for 54 days during the second half of the growing season of 1978. The simulated rainfalls of pH 5.25 and 3.17 provided calculated mean weighted pH values of 4.25 and 3.47 as compared with an ambient rainfall pH of 4.09.

A third experiment (Experiment 3) was performed at Upton, N.Y.

(Evans et al., 1983). Two simulated rainfalls of 12.7 mm each provided 25.4 mm of water weekly for 15 weeks. Each simulated rainfall occurred during 1.75 hours between 1800 and 2400 hours. The crop received no measurable water from ambient rain because it was covered during every ambient rainfall. All treatments received the same amount of water. Four replicates of four treatments of simulated rainfalls of pH 5.6, 4.1, 3.3, and 2.7 were arranged into latin squares. The field-plot design included eight complete latin squares yielding a total of 32 plots per treatment with four rows per plot. In this experiment, plants were shielded from all ambient rainfalls by two 30 × 10 m moveable rainfall exclusion shelters. All four rows of each plot were exposed to simulated rainfalls.

A fourth experiment (Experiment 4) was also performed at Upton, N.Y., during the summer of 1981 (Evans et al., 1983). Four replicates of four experimental treatments of simulated rainfalls of pH 5.6, 4.1, 3.3, and 2.7 were arranged into latin squares. The field plot design included eight latin squares yielding a total of 32 plots per treatment. These plants were not shielded from ambient rainfalls. The weighted mean acidities of all precipitation on plants exposed to ambient rain plus simulated rainfall treatments of pH 5.6, 4.1, 3.3, and 2.7 were equivalent to pH 4.07, 4.04, 3.92, and 3.64, respectively. Plants received three weekly exposures (between 0800 and 1200 hours) to simulated precipitation in sufficient quantities to wet the foliage only. These simulated rainfalls added only 16.7 mm more water than ambient rainfalls (211.6 mm) throughout the growing season. Each simulated rainfall provided water similar to the mode of all ambient rain showers (Evans et al., 1981b, 1982a).

Different conclusions have been drawn from results of these four individual experiments with field-grown soybeans. In Experiment 1 (Jacobson et al., 1980; Troiano et al., 1983) soybean seed yields were not significantly related to rainfall acidity in either filtered or unfiltered air. In Experiment 2 (Irving and Miller, 1981), simulated acidic precipitation also produced no statistically significant effect on seed yield. However, decreases in soybean yields due to acidic precipitation were observed in the other two experiments (Experiments 3 and 4; Evans et al., 1983, 1984a). An analysis of variance of selected subsets of one, two, four, and eight latin squares of Experiment 3 provides some insight on field variability (Evans and Thompson, 1984). The eight latin squares analyzed as individual experiments (four plots per treatment) yielded erratic conclusions. Statistically significant linear comparisons were detected in four of the eight latin squares. When two randomly selected latin squares (eight plots per treatment) were used in the analysis of variance, the linear component was just significant at the 1% level. When four latin squares (16 plots per treatment) were used, the linear component was highly significant (<0.001). When eight latin squares (32 plots per treatment)

were combined, the evidence that the treatment differences may be attributed to a linear gradient is overwhelming (<0.001). The low probability value (0.0033) for differences among latin squares indicates that field locations are a legitimate source of stratification. These results demonstrate that inadequate replication may result in a failure to detect biologically significant differences.

The most important difference in these experiments is their statistical designs. Two of the field layouts (Experiment 1, Troiano et al., 1983; and Experiment 2, Irving and Miller, 1981) used only one plot per treatment. These provided no replication except in the sense of plants, rows, or sectors within the single plot. Such studies are subject to the criticism that treatment effects cannot be separated from other microenvironmental variables peculiar to a specific plot location. Experiments 3 and 4 (Evans et al., 1983, 1984a) were highly replicated. They were designed to detect differences in 10% or less among treatment means. Type 1 error, α , was predetermined, and replication was sufficient to keep type 2 error low. This design was made possible because a preliminary experiment was available to estimate the expected components of variance. Despite differences in the procedures and protocols among the four experiments, it is primarily the quality of the experimental design which determines their validity and relative utility for crop-loss assessment.

Simulated acidic rainfalls may also affect product quality. In three experiments (one during 1979 and two during 1981) the total protein contents of soybean seeds was lower in plants exposed to simulated acidic rainfalls than to rainfalls of pH 5.6. In one experiment in 1982 no significant differences in protein occurred among the treatments used (Evans et al., 1984c). Mean protein contents of control plants for the three experiments reported herein were (33.0, 39.3, and 43.8%) comparable to protein yields of commercial soybean growers. Changes in protein content per seed mass were independent of reductions in seed mass per plant due to increased rainfall acidity. When results were expressed as protein content per plant, decreases in protein of 20% were common in plants exposed to rainfalls similar to ambient (pH 4.1) compared with experimental controls (pH 5.6).

V. Effects of Acidity on Lower Plants, Bacteria, and Plant Pathogens

Most multicellular organisms that have evolved from aqueous environments onto dry land have evolved specialized surfaces to retard desiccation. Present evidence indicates that organisms with protective coverings are less sensitive to acidity of rainfall than organisms that lack these coverings. For example, bacteria and other single-celled organisms are very sensitive to pH changes. Prokaryotic organisms survive within

a smaller range of pH levels than most multicellular organisms (Adler and Templeton, 1967; Ogiuti, 1936; Shoesmith, 1960). Motility of most procaryotic organisms is greatest between pH 6.8 and 9.0. Motility has been used as a measure of survival in such organisms. A 50% decrease in the velocity of flagellar movement occurred in *Bacillus brevis* when the pH was reduced from 7.5 to 5.0. Hoeninger (1965) showed that a pH decrease results in an increase in abnormal wave motions in flagella of *Proteus*. Below pH 5.0 almost all motility ceased.

Fertilization and spermatozoid motility in gametophytes of bracken fern are very sensitive to low pH and additions of sulfate, nitrate, and chloride (Evans, 1979). Spermatozoid motility at pH levels 6.0, 5.5, and 5.1 was about 70%, 50%, and 30%, respectively, of values obtained at pH 6.1, 2 to 4 minutes after exposure. Motility at sulfate concentrations of 43.3, 86.6, and 173.2 μM at pH 6.1 was about 60%, 45%, and 35%, respectively, of values obtained with no sulfate additions. Fertilization decreased as pH decreased below pH 6.1 (buffers of pH 6.1 in the absence of sulfate, nitrate, and chloride was considered the experimental control). Fertilization after 3.5 hours exposure to pH 5.5, 5.1, and 4.5 was about 90%, 75%, and 60%, respectively, of values obtained at pH 6.1. Fertilization values at sulfate concentrations of 43.3, 86.6, and 173.2 μM at pH 6.1 were about 85%, 75%, and 60%, respectively, of values obtained with no sulfate additions (Evans, 1979). Similar results were present in a forest at Brookhaven National Laboratory (Evans and Conway, 1980). Experimental results with bracken fern were similar to results of megaspore germination and sporophyte formation in the heterosporous fern, *Marsilea vestita* (Mahlberg and Yarus, 1977). Germination of megaspores was much more sensitive to low pH than was sporophyte development.

Photosynthesis in the caribou lichen *Cladina stellaris* (Opiz) is affected by the chemistry of simulated rainfall solutions (Lechowicz, 1982). When dried tissues were exposed to simulated rainfalls of pH 5.6, maximal rates of photosynthesis occurred in about 6 hours. Tissue wettings with low sulfate (5.5 μM) simulated rain of pH 4.0 resulted in photosynthesis rates 43% below controls 6 hours after wetting. Similar results were obtained at high sulfate concentrations (104 μM). Although such lichens are a major winter food resource for caribou and reindeer (Bergerud, 1977; Hanson et al., 1975) the overall impact(s) of the documented decreases in photosynthesis remains unknown.

Many microorganisms inhabit the surfaces of higher plants. A particular microorganism may have a positive (beneficial), negative (pathogenic), or neutral influence upon normal plant growth, development, and reproduction (see reviews by Dickinson and Preece, 1976; Preece and Dickinson, 1971). Leaf surface bacteria within a canopy of Douglas-fir may fix significant amounts of nitrogen (Jones, 1976). Many pathogens can

reduce crop yields substantially (Ridgway et al., 1978; Shaw, 1979). Effects of air pollutants on relationships between host plants and their leaf-surface microbes have been reviewed (Smith, 1976). An air pollutant may differentially influence host and microorganism as well as their interactions (De Sloover and Le Blanc, 1968; Saunders, 1973; Smith, 1976).

Germane experiments with simulated rainfalls highlight these interactions. Simulated acidic rain (pH 3.2) produced an 86% inhibition of *Cronartium fusiforme* telia on willow oak (*Quercus phellos*) compared with pH 6.0 under greenhouse conditions (Shriner, 1977). Halo blight caused by *Pseudomonas phaseolicola* on leaves of greenhouse grown *Phaseolus vulgaris* was stimulated or inhibited by simulated acidic rain depending upon the stage of disease development when rainfall occurred. Simulated acidic rain inhibited initial disease infection but stimulated disease development after infection had occurred which increased host injury.

In field experiments (Shriner, 1977), kidney bean plants that received simulated rainfalls of pH 3.2 had 34% as many nematode eggs per root system as plants that had received simulated rain of pH 6.0. All plants received ambient rainfalls in addition to simulated rainfalls. Plants that had received the low pH rainfalls had only 48% as much root surface galling as plants that received pH 6.0. Biomass of roots, shoots, and pods as well as soil pH were not significantly affected by the simulated rain treatments. Bean leaf area injury caused by bean rust (*Uromyces phaseoli*) was not consistently affected by simulated rainfall acidity under field conditions. There are no experimental field data that demonstrate that rainfall acidity affects host-pathogen relations that result in significant changes in plant productivity or survival.

VI. Indirect Effects on Vegetation: Soil Effects

The actual and potential effects of acidic deposition on soils and the impacts of soil systems on freshwater chemical changes have been reviewed elsewhere (Bache, 1980; Evans et al., 1981a; Johnson et al., 1982; McFee, 1983; Reuss, 1978). These reviews will provide a basis for an understanding of how changes in soil chemistry may impact upon terrestrial vegetation.

A. LEGUME-RHIZOBIUM INTERACTIONS

Since acidic rainfalls may affect host-parasite relationships, they may affect legume-*Rhizobium* relationships. Numbers of nodules per plant were reduced when soybean and kidney bean plants were exposed to simulated rainfalls of pH 3.2 under either field or greenhouse conditions. However, the reduced number of nodules per plant did not result in

decreased shoot, roots, or pods in most experiments (Shriner and Johnston, 1981). Nodulation of red clover and birdsfoot trefoil was also sensitive to simulated acidic rainfalls when plants were grown in soils obtained from Panther Lake and Woods Lake watersheds of the Adirondack region of New York. Nodulation was not affected in one study where an agricultural soil was used (Chang and Alexander, 1983). In all three soils, the dry mass and nitrogen contents of roots and tops were significantly lower from experimental plants compared with controls. These results are consistent with results of some field experiments with field-grown soybeans that show reduced seed yields and seed protein contents after exposure to high acidity rainfalls (Evans et al., 1981b, 1983).

B. SOIL MICROBIOLOGY

Soil microorganisms are critical to ecosystem function and the well-being of plants, animals, and humans. They are responsible for transformations of various elements and occupy a central role in the C, N, P, and S cycles. If there is a significant impact of acidic precipitation on soil microbial processes then a potential would exist for reduced productivity in unmanaged range and forest soils. Microbial growth is reduced by soil acidification (Francis et al., 1980). Normal functioning of plants, soils, and biological communities will be affected when a significant change in soil pH is observed due to acidic precipitation. Various soil types may respond to acidic rain differently with or without a change in soil pH.

The effects of acidification on forest litter decomposition vary with type of materials studied. Exposure to rainfalls of pH 3.0 increased the rate of decomposition of lodgepole pine needles compared with needles exposed to rainfall of pH 6.5 (Abrahamsen et al., 1980). Applications of acid to pine needles in litter bags in field plots also stimulated decomposition (Roberts et al., 1980). In contrast, no changes in decomposition rates were detected for either spruce needles or aspen sticks (Abrahamsen et al., 1980).

Acidic rain applications significantly reduced organic matter decomposition in forest soils where increases in soil acidity were observed (Abrahamsen et al., 1980; Baath et al., 1980; Francis et al., 1980). With a slight decrease in soil pH after applications of rainfall of pH 2.5, rates of cellulose decomposition were decreased. The rate of decomposition of humus decreased significantly with increased acidification.

Effects of acidity on microbial decomposition of oak leaves in naturally acid and acidified soils were studied (Francis et al., 1980). There was a 52% decrease in total CO₂ production in the pH-adjusted acid soil compared with a natural control soil (pH 4.6). Highly significant differences ($p < 0.01$) in CO₂ production were observed among soils amended with

organic matter. A 37% reduction of total CO_2 evolution was observed in the acidified (pH 3.5) soil. Moreover, there was a significant ($p < 0.01$) correlation between the amount of CO_2 produced and the exchangeable H^+ content of the soil (Francis et al., 1980).

Organic nitrogenous compounds in soils, sediments, plants, and animals are converted to ammonium ion (ammonification) by a large group of heterotrophic bacteria, fungi, and actinomycetes. Ammonification was inhibited by acidification of some soils (Francis et al., 1980). Ammonification in a pH-adjusted acidic soil (pH 3.5) was about half that of a naturally acidic soil (pH 4.6). Highest rates of ammonification were observed in the pH-adjusted neutral soil (Francis et al., 1980). However, ammonification is much less sensitive to acidification than is nitrification (Dancer et al., 1972).

Nitrification is the sequential oxidation of ammonia to nitrite and then to nitrate by autotrophic and heterotrophic microbial communities. Autotrophic nitrification rates are ten times greater than heterotrophic nitrification rates. Autotrophic nitrification is principally accomplished by *Nitrosomonas* sp. and *Nitrobacter* sp. These organisms derive energy for growth from the oxidation of inorganic nitrogen compounds. Nitrification occurs optimally at neutral to slightly alkaline pH levels. Nitrification in acid soils is inhibited and nitrifying organisms are eliminated at high acidities (below pH 5.0). In acid environments, nitrification proceeds slowly, even in the presence of an adequate supply of substrate, and responsible species are rare or totally absent at high acidities. Typically, nitrification decreases markedly below pH 6.0 and becomes negligible below pH 5.0 (Dancer et al., 1972), yet nitrate may occasionally be present in field soils of pH 4.0 and below (Alexander, 1977). Some soils nitrify at pH 4.5 while others do not. The differences in response may be attributed to acid-adapted strains or to chemical differences in the two habitats. Neutral to alkaline soils have large nitrifier populations (Alexander, 1977). Accumulation of nitrate has been observed in acidic soils as low as pH 3.9 (Weber and Gainey, 1962). However, Walter and Wickramasinghe (1979) isolated pure cultures of ammonium-oxidizing autotrophic, nitrifying bacteria from acid soils of pH 4.0 to 4.5. Nitrite-oxidizing bacteria were detected in several acid soils but pure cultures were not isolated.

Soil bacteria are known to reduce nitrates to N_2 gas under anoxic conditions in the presence of available C (denitrification). Of particular interest is the biogenic emission of N_2O and its subsequent effect in the depletion of atmospheric O_3 or its contribution to the formation of nitrate in the atmosphere. Soil pH is known to affect the rate and the composition of the gaseous end products of denitrification. Recently, Francis et al. (1980) reported that denitrification was rapid at soil pH 6.5 with little

N_2O detected, indicating complete denitrification whereas in acid (pH 4.6) and acidified (pH 3.5) soils, N_2O was the major end product.

It may be speculated that further acidification of acid forest soils by acidic rain is perhaps a very slow process. Many years may be required for acidic rain to change the soil pH. Rapid adaptability of microbial populations to changing physical and chemical environments and substantial differences in the measured soil pH versus the actual pH in the microsite environments make accurate monitoring of short-term changes that might be caused by acidic precipitation very difficult. It may also be speculated that slow acidification may affect soil microbial communities which may gradually result in the selection of acid-resistant or tolerant organisms or elimination of certain species. On a long-term basis, acidic rain may affect certain key processes catalyzed by soil microorganisms such as organic matter decomposition, and N transformation and ultimately the nutrient cycling in the forest ecosystem. More research from field experiments is needed before the impacts of acidification of soils on soil microbiological processes vital for nutrient cycling and ecosystem function can be evaluated.

VII. Effects on Freshwater Biota

A. FRESHWATER ACIDIFICATION

The effects of atmospheric deposition on freshwater acidification and the biotic impacts of this acidification have been reviewed in detail elsewhere (Evans et al., 1981a). Some important aspects of this review will be discussed herein. Synoptic surveys (one or a few samples collected in a short period of time from each of many lakes) in Norway (Braekke, 1976; Wright and Henriksen, 1978), Sweden (Dickson, 1975; Hörnström et al., 1973; Odén, 1976), Scotland (Wright and Henriksen, 1980), the northeastern United States (Davis et al., 1978; Schofield, 1976a) and southeastern Canada (Conroy et al., 1976) all indicate the widespread acidification of low conductivity, oligotrophic lakes in regions receiving acidic precipitation. Extensive studies, involving many observations in one lake or in each of many lakes in these regions, confirm these synoptic studies.

Acidification of these low conductivity, oligotrophic lakes in the above-mentioned locations has occurred in a short period of time, the past few decades. The rapid rate of this acidification is demonstrated both by actual measurements of temporal changes in water chemistry and by the disappearance of fish. Fresh waters which formerly supported natural fish populations have become so acidic and Al contaminated, a consequence of watershed acidification (Cronan and Schofield, 1979), that fish cannot

survive (Almer et al., 1974; Braekke, 1976; Davis et al., 1978; Hendrey and Vertucci, 1980; Scheider et al., 1979; Schofield, 1976).

The acidification of freshwaters is associated with a general increase in sulfate and/or nitrate concentrations of precipitation in the impacted areas (Beamish, 1976; Braekke, 1976; Likens et al., 1979; Odén, 1976). Regional patterns of lake-water chemistry reflect regional patterns in precipitation chemistry (Braekke, 1976; Henriksen, 1979; Wright and Henriksen, 1980; Wright and Snekvik, 1977). Furthermore, many streams and lakes in such areas also have rapid pH fluctuations due to acid deposition either directly as episodes of low pH rain or indirectly, following snow melting and the release of atmospheric pollutants stored in the snow pack (Braekke, 1976; Hendrey et al., 1980a; Henriksen and Wright, 1977; Hultberg, 1976; Jeffries et al., 1979; Scheider et al., 1979).

B. BIOTIC EFFECTS—NON-FISH

Inhibition of microbial decomposition can have profound effects throughout an aquatic ecosystem on detritus removal, conservation of energy, nutrient recycling, primary production, and detritivore production. Production at higher trophic levels may be affected by changes in microbial activity. Several investigations have indicated that microbial decomposition is greatly inhibited at pH levels commonly encountered in lakes affected by acidic precipitation (Hendrey et al., 1976). Neutralizations of acidified lakes in Canada resulted in a significant increase in aerobic heterotrophic bacteria in the water column (Scheider et al., 1975). Organic litter accumulation is accelerated in acidified waters (Grahn et al., 1974; Harrison, 1958; Hendrey et al., 1976; Sutcliffe and Carrick, 1973).

Reduction of microdecomposer activities may have a direct effect upon invertebrates by altering their food supply. Although certain benthic invertebrates appear to feed directly on allochthonous detritus material, it seems that "conditioned" (colonized by microorganisms) material is preferred, and that the nutritional value of the detritus is highly increased by conditioning (Boling et al., 1975). Bacteria may also be a food source to be removed by the filtering apparatus of organisms such as Calanoida. An inhibition of microbiota or a reduction in microbial decomposition processes would therefore have a direct impact on the lakes' animal communities.

Aquatic macrophyte communities are altered by acidification causing changes in animal habitats and possibly affecting nutrient cycling. Plant growth and productivity (O_2 production) can also be reduced (Laake, 1976). In some acidic lakes in Sweden, Norway, in the Adirondack Mountains, and in acid mine drainage waters (Drabløs and Sevaldrud, 1980;

Grahn, 1976; Harrison, 1958; Harrison and Agnew, 1962; Hendrey and Vertucci, 1980; Scheider et al., 1975), unusually dense mats of *Sphagnum* occur. Many other acidic, clearwater lakes do not have abundant amounts of *Sphagnum*. In developing their hypothesis on oligotrophication, Grahn et al. (1974) stressed two biologically important consequences of this *Sphagnum* expansion. First, *Sphagnum* has an ion-exchange capacity which results in the withdrawal of base ions such as Ca^{2+} from solution, thus reducing their availability to other organisms. Secondly, dense growths of *Sphagnum* form a distinct biotope which is unsuitable for many members of the bottom fauna.

Dense growths of attached algae occur on the bottoms of acidified lakes and streams. Under some acidic conditions, unusual accumulations of algae may occur. In Swedish lakes, *Mougeotia* and *Batrachospermum* become important components of the benthos. Lime treatment caused a rapid decomposition of organic litter as well as great reductions of the algal mat, indicating that an inhibition of bacterial activities had taken place at low pH (Almer et al., 1978; Andersson et al., 1975; Grahn et al., 1974; Hultberg, pers. comm.). In artificial stream channels in Tovdal, Norway, and in a natural stream in the Hubbard Brook Experimental Forest, extensive growths of filamentous algae resulted upon acidification (pH 4.0) with H_2SO_4 (Hall et al., 1980; Hendrey et al., 1976). Several factors may contribute to these unusual accumulations of certain algae. Intolerance of various species to low pH or to consequent chemical changes will allow just a few algal species to utilize nutrients available in these predominantly oligotrophic waters (Moss, 1973). Many species of invertebrates are absent at low pH, and removal of algae by grazing is probably diminished (Hall et al., 1980; Sutcliffe and Carrick, 1973). It is hypothesized that the increased algal growths are due, in part, to the reduction of invertebrate grazing activity (Hendrey et al., 1980).

In many lakes free-floating algae, or phytoplankton, form the base of the food chain. The process of algal growth (primary productivity) is regulated by several factors including nutrient availability, light penetration, and grazing by small aquatic animals (zooplankton). All of these factors are altered by lake acidification. Species composition of phytoplankton is altered by acidification and the number of species decreases. However, there is no consistency among various investigations as to which taxa are likely to be dominant under conditions of acidification. Pyrrophyta may be more common (e.g. species of *Peridinium* and *Gymnodinium*) than others in lakes near pH 4. With decreasing pH in the range of 6 to 4, many species of Chlorophyta are eliminated, although tolerant forms are found in the acid range.

It has been demonstrated that watershed acidification greatly increases Al leaching (Cronan and Schofield, 1979; Gjessing et al., 1976) and several

studies taken together support the notion that increased Al in soil pore water may reduce total P loading (Hendrey et al., 1980b). While less P may be removed at fixed Al concentrations below pH 5 than at pH 5 to 6 (Almer et al., 1978), an elevated concentration of Al may result in an increase in P removal below pH 5, by whatever means, not only in the lake water but in the watershed soil as well. This topic needs further investigation.

Zooplankton community composition is simplified with species number decreasing in acidified waters, but effects on biomass are not well documented (Almer et al., 1974; Hendrey and Wright, 1976 and Parsons, 1968). The distributions and associations of crustacean zooplankton are strongly related to pH and to the number of fish species present in the lakes. Food supply, feeding habits, and grazing of zooplankton are probably altered following acidification, as a consequence of decreased biomass and species composition of planktonic algae and bacteria. Studies of zooplankton have not been sufficiently intensive to assess whether acidification results in reduction of zooplankton standing stocks.

Bottom-dwelling (benthic) invertebrate communities are simplified with numbers decreasing in acidified waters, and biomass may also decrease. Surveys at many sites receiving acidic precipitation in Norway, Sweden, Great Britain, and North America have shown that waters affected by acidic precipitation have fewer species of benthic invertebrates than less acidic localities (Almer et al., 1974; Borgström et al., 1976; Conroy et al., 1976; Hendrey and Wright, 1976; Økland, J., 1969; Sutcliffe and Carrick, 1973). Some species, such as the amphipod *Gammarus lacustris*, which is an important element in the diet of trout in Norwegian lakes where it occurs, cannot tolerate exposure to pH 5.0 for 24 to 48 hours (Borgström and Hendrey, 1976; Økland, K., 1969). These kinds of data are not available for most fish-food organisms.

Quantitative data concerning the effects of low pH on the benthic fauna available for some acidified Norwegian lakes showed notably low standing crops (Hendrey et al., 1976), but a few species are favored by conditions in acidified waters. The Notonectidae (backswimmer), Corixidae (water boatman) and Gerridae (waterstrider) are often abundant in acidified soft waters at pH as low as 4.0. This may, in part, be due to lack of fish predation. Chironomids have been found to be the most common animal group in acidic lakes (Raddum, 1978, 1980) and may provide the food base for carnivorous invertebrates which are abundant in the absence of fish predation.

C. EFFECTS ON FISH

Fish have been eliminated from many fresh waters which have become acidified (Beamish and Harvey, 1972; Dochinger and Seliga, 1976; Lei-

vestad et al., 1976; Schofield, 1976). As a general rule, acidified lakes are fishless below pH 4.8. In the U.S. the most heavily affected region known is in the Adirondack Mountains. A survey of 217 lakes above 610 m elevation revealed 51% had pH values below 5. Of these acidic lakes 90% had no fish. In the period 1929 to 1937, only 4% of these lakes had a pH below 5 and were fishless (Schofield, 1976).

Very large geographic areas impacted by acidic precipitation have suffered reduction in fish stocks. This has been most clearly demonstrated in Sweden and Norway, where the number of fishless lakes is increasing yearly. The same appears to be true for southeastern Canada from Ontario to Nova Scotia. No comparable analysis of fish status exists for the eastern U.S. outside of the Adirondack Mountains.

Elimination of fish populations from lakes and rivers is primarily caused by reproductive failure. As young-of-the-year are eliminated and year classes fail in most acidic waters, older fish become larger due to reduced competition for remaining food supplies. Diet also changes as preferred prey are eliminated by acidification. Egg and fry mortality is the primary cause for reproduction failure (Almer et al., 1978; Leivestad et al., 1976; Peterson et al., 1980).

D. INTERACTION WITH ALUMINUM

Elevated levels of Al caused by watershed acidification have serious effects on fish. Watershed acidification results in elevated concentrations of Al in runoff waters to the range of 1 mg Al liter⁻¹. Laboratory studies show Al to be toxic to salmon at 0.2 mg liter⁻¹. Fish kills of cisco in two Swedish lakes impacted by acid deposition occurred when stream and lake water Al concentrations were 0.5 mg liter⁻¹ at pH 5.0 to 5.5. Fish-gill Al concentrations were seven to eight times higher than in gills of fish from uncontaminated lakes. Other factors, i.e. climatic, chemical, and biological also contributed to these fish kills (Grahn, 1980).

Aluminum ion speciation is an important factor in its toxicity to fish. Maximum toxicity of Al to brown trout tested over the pH range 4.0 to 6.0 and Al concentrations of 0.2 to 0.8 mg liter⁻¹ occurred at pH 5.0 with no toxicity observed at pH 4.0 and 6.0 (Leivestad et al., 1980). Aluminum forms strong complexes with OH⁻, F⁻, SO⁻² and dissolved organics. Additions of these materials in experiments with brook trout and white sucker eggs and fry at pH 4.0 to 5.5 and Al concentrations of 0.1 to 0.5 mg liter⁻¹ reduced or eliminated the toxic effects of Al (Baker and Schofield, 1980).

Toxic aluminum concentrations are associated with disturbed ion exchange over gills and with respiratory distress. Analysis of venous blood from brown trout exposed to 0.2 to 0.8 mg liter⁻¹ and pH 4.0 to 6.0 found a rapid loss of plasma Na⁺ and Cl⁻ occurred with Al toxicity. Addition

of Ca^{2+} reduced this ion loss. Massive mucous clogging of gills occurred and venous oxygen tension was lowered in these fish (Baker and Schofield, 1980).

VIII. Ecosystem Effects

Several field experiments have been conducted in forests. Perhaps the first field experiment to view effects of acidic rain on forests began in 1969 (Tamm, 1976). Sulfuric acid levels of 50, 100, and 150 $\text{g ha}^{-1} \text{yr}^{-1}$ were added to soils. Treatments usually included the presence and absence of supplemental irrigation and fertilization at 60, 120, and 180 $\text{g N ha}^{-1} \text{yr}^{-1}$, with and without acidic conditions. Although treatments of 100 g S as $\text{H}_2\text{SO}_4 \text{ ha}^{-1} \text{yr}^{-1}$ killed most of the ground vegetation such as mosses, lichens, and *Calluna vulgaris*, there was no evidence of a negative effect on tree stem volume growth. From these results, Tamm (1976) concluded that except in areas where forest trees exhibit visible pollution symptoms, ambient acidic precipitation and other types of atmospheric acidity have no effect on tree growth. However, it should be recognized that since only three plots per treatment (two plots per treatment in some experiments) were used, variations among plots could easily have overshadowed differences among treatments.

In contrast to the experiments of Tamm, other researchers in Sweden found a statistically significant difference in tree growth between areas exposed to acidity and areas more remote from transported atmospheric acidity (Jonsson, 1977; Jonsson and Sundberg, 1972). They concluded that there was no reason to attribute the growth reduction to anything other than acidic rain. In contrast, researchers in Norway (Abrahamsen et al., 1977) and the United States (Cogbill, 1977) have not detected any consistent decreases in tree growth within forests that could be attributed to acid deposition. Presently, the effects that precipitation acidity has on forest productivity remains unknown. More recently, a forest growth simulation model (Botkin and Aber, 1978) was used to estimate potential effects of acidic rain on forest ecosystems where only increases in foliar injury were considered. This model predicted that visible foliar injury up to 5.5% of leaf area would produce no decreases in total forest productivity. The results imply that a reduction of leaf area of 10–25% per year of one tree species would be required to reduce overall forest biomass. Below this 10–25% range a decline in productivity of one or more species could be compensated for by increased productivity of one or more other species.

Computer simulation exercises were performed to test some possible effects of acidic precipitation. The JABOWA computer model (Botkin and Aber, 1973) of forest growth was modified to include effects of pre-

precipitation acidity on nitrogen availability and tree growth. The model found a direct positive relationship between N availability and biomass accumulation (Aber et al., 1980). The relationships between forest production, litterfall, and litterfall decomposition were analyzed using the FORTNIT forest nitrogen model (Aber et al., 1980). The simulation model found lower rates of litter decomposition would be compensated by higher forest floor biomass accumulation so that N availabilities would not be greatly altered over a period of 15 to 40 years. After 40 years, slower litter decomposition rates would (according to the model) provide higher N availabilities due to the decomposition of the larger litterfall biomass. However, no field data are available to confirm these simulations (Aber et al., 1980). It seems obvious that only well-designed field experiments with an adequate level of replication to overcome natural variation will be needed to document alterations in natural ecosystems by acidic deposition, if present. Most published reports on altered forest productivity are subject to the criticism that other factors (biotic and abiotic) in the environment were not adequately controlled, documented, and/or accounted for. It is suggested that the use of moveable rainfall exclusion facilities on natural ecosystems may overcome the above criticism. Since variation in natural ecosystems may be greater than that in agricultural fields as many as 10–20 plots per treatment may be necessary to detect statistically significant differences among treatments of less than 10%.

IX. Overall Evaluation of Effects of Precipitation Acidity upon Terrestrial Vegetation

Presently there is evidence that the acidity in precipitation, at ambient levels, is having deleterious effects upon terrestrial vegetation. This statement is mostly derived from data of crops grown under field conditions. Experiments have been conducted under controlled-environmental conditions but since plant responses to acidic rain grown under such conditions differ from responses under field conditions, data from controlled environments may only point to mechanisms. Few field experiments have been conducted that are statistically capable of detecting significant differences among treatments. Although decreases in yields of various crops have been documented in controlled-environment and field experiments at pH levels of 4.0 or below, only well-designed field experiments will document changes in plant productivity or survival that may be expected from actual acidic rainfall exposures. It is essential that experiments using standard agronomic practices or total ecosystem considerations with large numbers of replicates be conducted so results can be extrapolated to actual crop or ecosystem situations, respectively. Large numbers of treatment replicates are needed to demonstrate differences (statistically significant) among treatments with means that differ by 10%.

To standardize results of future experiments, a uniform expression of data should be utilized. To date, the most meaningful relationships between rainfall acidity and plant responses have been obtained when responses are plotted as a function of the hydrogen ion concentration of the simulated rainfalls (Evans and Lewin, 1980; Evans et al., 1981b, 1983, 1984a). This expression or some other more meaningful expression should be used so data can be compared with ambient precipitation acidities.

Acidic precipitation may affect productivity of crop and forest plants by direct or indirect means (necrosis, soil nutrient effects, bacteria and fungi). If significant alterations in productivity of either crops or forest occur, significant financial impacts may result. Currently, evidence linking existing and/or anticipated levels of rainfall acidity to crop yield reductions is meager. From available data, it is clear that the level of injury, if injury occurs, is less than year-to-year changes in addition to other abiotic factors. This does not mean, however, that possible injuries from acidic precipitation should be ignored. It is important to determine even small changes in productivity. For example, a 1.0% reduction in yields of soybeans grown in the northeastern United States would represent a loss of 49.5 million dollars calculated for 1979 (ignoring price elasticity; Evans et al., 1981b, 1983, 1984a).

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