

Acute Effects of Acidic Fog on Photosynthetic Activity and Morphology of *Phaseolus lunatus*

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Abstract. Acute effects of high-nitrate/low-sulfate acidic fogs with a pH of 2.5 and 3.0 were investigated on 3.5- to 4-week-old *Phaseolus lunatus* L. in a series of replicated trials. After 24 hours, CO₂ assimilation rates of primary leaves were reduced by at least one-third by 3-hour fogs with a pH value of 2.5 as compared to control plants treated with a fog of pH 6.3. A 3-hour fog at pH 3.0 reduced CO₂ assimilation a minimum of 20%. Stomatal resistance increased in primary leaves of plants exposed to an acidic fog of pH 2.5 by >37% compared to plants subjected to pH 6.3 fogs. Stomatal resistances in leaves exposed to pH 3.0 fogs increased at least 27%. However, internal CO₂ concentrations were not significantly different between control- and acid-fogged plants at any pH. Standardizing plants for similar CO₂ assimilation rates allowed statistical separation of photosynthetically important variables as compared to unstandardized experimental designs with higher interplant variability. Methacrylate plastic sections of foliar lesions resulting from exposure to pH 2.0 fogs revealed that damage usually progressed vertically from the upper to lower epidermis. Xylem was less susceptible to damage than other tissues.

Research on the impact of acid deposition on vegetation has focused on acid rain rather than acidic fog. Typically, plant response to acid deposition includes lesion development, weathering of cuticular wax, foliar leaching, premature abscission, and abnormal growth or development (Cowling, 1982; Lee, 1982; Linthurst et al., 1982; Shriner, 1986). However, the effects of acid deposition can be neutral or even positive. Acidic fogs may have a greater impact on plants than acid rain because they often have a lower pH (Granett and Musselman, 1984; Johnson and Siccamo, 1983). The few studies specifically examining the impact of high nitrogen acidic fogs have focused on changes in plant nitrogen form and content (Trumble and Hare, 1989) or on secondary plant chemistry (Dercks et al., 1990).

In the Los Angeles Basin, ambient fogs contain considerably more nitric acid than the sulfate acidic fog studied in the eastern United States and routinely exhibit a pH of 2.0 to 3.0 (Hoffman, 1984). Although urban encroachment has reduced the total acreage of farmland in Orange and Los Angeles counties, the total value of field-grown crops in this area exceeds U.S.\$70 million an-

nually (Ivey and Johnson, 1986). Thus, potential economic losses due to air pollutants can be significant.

Although significant yield losses have led researchers to extensively investigate the impact of gaseous air pollutants on photosynthetic activity of affected foliage (Hällgren, 1984), acidic precipitation-induced alterations in photosynthetic activity have not been adequately studied. Further, results have been inconsistent regarding the effect of acidic rain

on photosynthesis: an early study reported a significant reduction in photosynthesis in moss (Sheridan and Rosenstreter, 1973), whereas others report increases in photosynthesis in *Glycine max* L. (Irving, 1979) and *Phaseolus vulgaris* L. (Ferenbaugh, 1976).

The morphological effects of high nitrogen acidic fogs on leaves are not well known, but studies with simulated sulfate acid rain have described a sequence of cellular collapse progressing from the upper to lower epidermis of *P. vulgaris* (Evans et al., 1977). More recently, necrotic lesions have been created on several crops with a high-nitrate/low-sulfate acidic fog under laboratory conditions (Granett and Musselman, 1984; Granett and Taylor, 1981). Thus, our objectives were to: 1) evaluate the acute impact of short-term acidic fogs on photosynthetic activity of *P. lunatus* L. and 2) document the acute morphological effects of short-term acidic fogs.

Simulated acidic fogs. Simulated acidic fogs of pH 2.5, 3.0, and 6.3 (control) were prepared with reagent-grade nitric and sulfuric acid as described by Trumble and Hare (1989). Key ionic components were added (Waldman et al., 1982). Fogs were created within 1-m³ chambers using an apparatus designed by Musselman et al. (1985) operated at 703 kPa. The chambers were placed in a temperature-controlled greenhouse equipped with activated charcoal filters. Temperatures during fogging ranged from 22 to 25°C. A shade cloth over the chamber prevented light intensities from exceeding 300 μmol·m⁻²·s⁻¹, closely simulating light conditions during an acidic fog episode. *Phaseolus lunatus* ('Henderson Bush') were fogged for 3 h, left in the shaded chambers to dry for 2 to 3 h (22 to 25°C), and then moved to greenhouse benches. To avoid any chamber effects, the

Table 1. Acute effect of acidic fog on CO₂ assimilation, stomatal conductance, and internal CO₂ concentrations in primary leaves of *Phaseolus lunatus*^a.

pH of fog	Replicate (no.)	Response of plants		Percent change	Paired <i>t</i> value	<i>P</i>	Unpaired <i>t</i> value	<i>P</i>
		Controls	Fogged					
<i>CO₂ assimilation (mg·s⁻¹·m⁻²)</i>								
2.5	1	0.481	0.263	-45.32	5.26	0.001	5.53	0.0001
	2	0.419	0.158	-62.29	6.00	0.001	6.81	0.0001
	3	0.560	0.375	-33.04	3.97	0.004	3.99	0.001
3.0	1	0.496	0.303	-38.91	4.37	0.002	4.46	0.0001
	2	0.456	0.300	-34.21	5.33	0.0001	3.70	0.002
	3	0.583	0.464	-20.41	2.50	0.034	2.50	0.022
<i>Stomatal resistance (s·cm⁻¹)</i>								
2.5	1	2.217	3.772	41.22	2.69	0.031	3.32	0.004
	2	2.277	5.251	56.64	6.23	0.001	5.82	0.0001
	3	2.584	4.109	37.11	2.96	0.018	2.75	0.014
3.0	1	2.149	3.364	34.90	2.56	0.031	2.77	0.013
	2	2.064	3.111	33.66	4.93	0.001	3.57	0.002
	3	2.387	3.277	27.16	1.83	0.100	1.95	0.068
<i>Internal CO₂ concentration (ppm)</i>								
2.5	1	336	315	-6.35	1.80	0.114	1.80	0.091
	2	341	320	-6.23	1.63	0.154	1.69	0.112
	3	291	280	-3.71	0.72	0.493	0.75	0.464
3.0	1	304	316	3.92	1.47	0.175	1.41	0.176
	2	331	323	-2.54	0.82	0.436	0.94	0.362
	3	286	269	-5.65	1.25	0.242	1.53	0.144

^aPost-treatment comparisons of 10 pairs of plants with primary leaves exhibiting similar photosynthetic rates (± 0.003 mg CO₂/sec per m²) before exposure to fogs. Data collected 24 h after treatment under metal halide light providing a minimum of 1000 μmol·m⁻²·s⁻¹.

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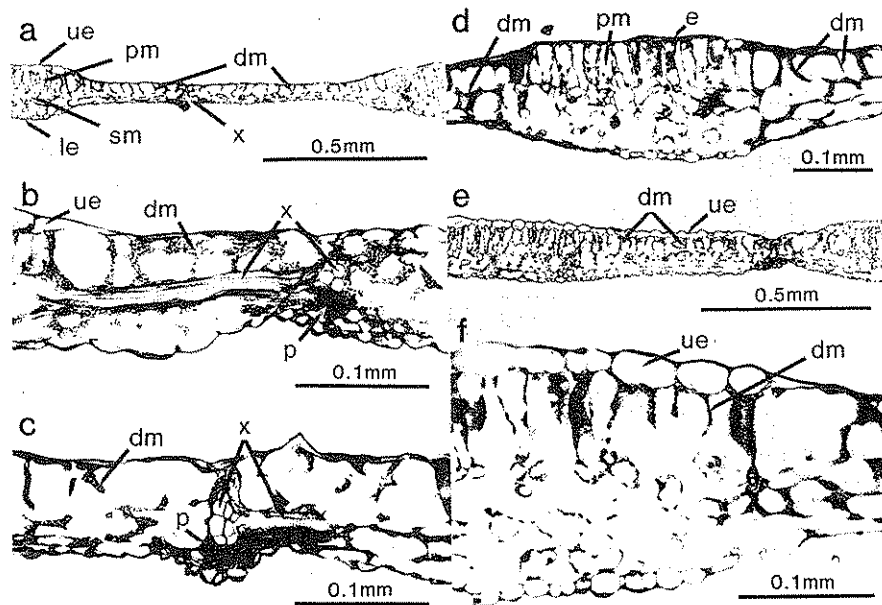


Fig. 1. (a) Low-magnification micrograph of acidic fog damage to *Phaseolus lunatus*. Both upper and lower epidermal cells are obliterated in the area of the lesion, in contrast to well-formed upper (ue) and lower epidermal cells (le) in the healthy regions adjacent to the lesion. Damaged palisade and spongy mesophyll (dm) in the lesion are shrunken and dark-staining with no organelles visible, in contrast to healthy palisade (pm) and spongy mesophyll (sm) adjacent to the lesion. Xylem tissue (x) did not collapse even in the center of the lesion. (b,c) Xylem tissue (x) was structurally intact in the lesion. Phloem (p) tissue collapsed. Damaged mesophyll (dm) was shrunken, without visible organelles, and stained dark with a grainy texture. Most of the upper epidermis was obliterated over the lesion, but a partially collapsed upper epidermal cell (ue), which does not exhibit the dark staining pattern characteristic of damaged mesophyll, is visible in (b). (d) Apparently undamaged palisade mesophyll (pm) beneath an obliterated epidermis (e). (e) An exceptionally extensive area of damaged mesophyll (dm) beneath an apparently undamaged upper epidermis (ue). (f) Damaged palisade mesophyll (dm) found beneath an apparently undamaged upper epidermis at the margin of a lesion (main area of lesion was to the right of the micrograph where both the epidermis and mesophyll were destroyed).

treatments (pH 2.5, 3.0, and 6.3), following an initial randomization, were rotated through each of the chambers in consecutive replicates.

Acidic fog effects on photosynthesis and stomatal resistance. *Phaseolus lunatus* from a single seed lot per replicate were germinated in the greenhouse in UC mix (Matkin and Chandler, 1957) and fertilized twice weekly with one-half strength Hoagland's nutrient solution (Downs and Hellmers, 1975). When all plants had the primary leaves fully expanded (≈ 3.5 to 4 weeks old), a primary leaf of each plant was examined for apparent CO_2 assimilation and stomatal conductance using a LI-COR 6250 Photosynthesis Measurement System (LI-COR, Lincoln, Neb.). Initial measurements were made 24 h before treatment in the laboratory (22 to 24°C) under a metal halide lamp providing a minimum of $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. All plants were allowed to acclimatize to laboratory conditions under a metal halide light for ≈ 30 min before examination. Leaf temperatures throughout the study averaged $25.3 \pm 1.3\text{C}$ (sd).

After sampling 80 to 120 plants, 20 pairs of plants were identified in which each pair differed in CO_2 assimilation rate in the primary leaves by $< 0.003 \text{ mg CO}_2/\text{sec per m}^2$. Standardizing test plants by matching CO_2 assimilation rates was considered potentially important because even plants from the same seed lot grown concurrently under green-

house conditions may vary significantly in photosynthetic activity (Trumble et al., 1985). One of each pair of plants with comparable photosynthetic rates was exposed to a control fog, and the other to an acidic fog. Ten pairs of plants were examined for each pH value of the acidic fog. Post-treatment photosynthesis measurements were taken under a metal halide lamp 24 h after completion of fogging. This test was replicated three times.

Although data from this experiment could be analyzed using either paired or unpaired *t* tests, pairing plants based on pretreatment photosynthetic rates could reduce between-plant variability. Therefore, a second experiment was designed to determine if such pairing would improve statistical detection of physiological differences occurring in response to treatment. In this experiment, plants that were not photosynthetically paired were randomly assigned to treatment or control fogs (10 each in pH 2.5 and control fogs; 10 each in 3.0 and control fogs). This second experiment was replicated twice. Again, to minimize potential chamber effects, chamber assignments were initially randomized for the first replicate and then changed for the next replicate.

Analysis of changes in CO_2 assimilation rates ($\text{mg CO}_2/\text{sec per m}^2$), stomatal resistances ($\text{s}\cdot\text{cm}^{-1}$), and internal CO_2 concentrations (ppm, after von Caemmerer and Farquhar, 1981) between test and control plants were made using both paired and un-

paired *t* tests (Expt. 1) and an unpaired *t* test (Expt. 2). To determine the importance of a paired *t* test analysis for the plants standardized by CO_2 assimilation rate in Expt. 1, correlations between test and control plants within replicates were generated for each physiological variable studied (Snedecor and Cochran, 1978). Coefficients of variation also were determined for CO_2 assimilation rates in Expts. 1 and 2. Statistical analyses among replicates were not considered due to expected variation of plants between replicates within fog treatments. Preliminary studies indicated variability occurred in response to changes in glasshouse conditions between replicates, as well as the slight variation in plant ages tested (3.5 to 4 weeks) between replicates.

Acidic fog effects on leaf morphology. Four- to 6-week-old plants were used for examining fog effects on the morphology of primary and trifoliolate leaves. In the first study, 12 plants were evaluated that varied in developmental stage from flower bud initiation to early fruit production (fruit ≈ 1 cm long). From each plant, one primary leaf and one trifoliolate leaflet (usually the apical leaflet) were selected for use. The selected trifoliolates ranged from the oldest to the third oldest trifoliolate on the plant, and the average length and maximum width of their apical leaflets was $85.3 \pm 3.6 \times 53.7 \pm 2.1$ mm, respectively ($\bar{x} \pm \text{SEM}$). In the second study, there were six plants that were not yet flowering. One primary leaf and one trifoliolate (either the oldest or second oldest trifoliolate) on each plant were selected for measurement (apical leaflet averaged $100.3 \pm 5.3 \times 63.3 \pm 4.7$ mm; length \times width, $\bar{x} \pm \text{SEM}$).

One day before treatment, the selected leaflet of the trifoliolate and a delineated area on the selected primary leaf from each plant were microscopically examined. During this pretreatment examination, all pre-existing scars and lesions (> 0.3 mm in diameter) similar in appearance to acid fog-induced lesions were marked to ensure that pre-existing lesions would not be confused with those resulting from treatment. An equal number of plants were assigned randomly to control and treated groups. The following day, control plants were exposed to a pH 6.3 fog for 2 h and treated plants were exposed to a pH 2.0 fog for 2 h.

The selected leaves were removed from the plants 22 to 30 h after fogging, examined microscopically, and the number of new lesions was recorded for each leaf. Pieces of leaf tissue were cut from the selected leaves with a razor and placed in fixative [2% glutaraldehyde in 0.1 M pH 7.2 Sorensen buffer (Berlyn and Miksche, 1976)], usually within 5 min of removing the leaf from the plant. Each leaf piece from treated plants had a new lesion that was visible on the adaxial surface and was more than 0.3 mm across. Leaf pieces from control plants had no new lesions. Fixed leaf tissue was dehydrated in a series of concentrations of ethanol (10% to 95%), infiltrated, and embedded in glycol methacrylate plastic (JB-4 embedding kit, Polysciences, Warrington, Pa.). Sections (4μ thick) were

Table 2. Acute effect of acidic fog on CO₂ assimilation, stomatal conductance, and internal CO₂ concentrations in primary leaves of unpaired *Phaseolus lunatus*^a.

pH of fog	Rep. (no.)	Responses of plants		Percent change	Unpaired <i>t</i> value	<i>P</i>
		Control	Fogged			
<i>CO₂ assimilation (mg·s⁻¹·m⁻²)</i>						
2.5	1	0.423	0.347	-22.70	1.36	0.191
	2	0.446	0.383	-14.13	1.55	0.138
3.0	1	0.412	0.482	-14.52	2.01	0.060
	2	0.450	0.500	11.11	1.63	0.121
<i>Stomatal resistance (s·cm⁻¹)</i>						
2.5	1	2.837	4.105	30.89	1.61	0.126
	2	2.495	2.774	9.07	0.49	0.629
3.0	1	2.320	2.884	19.56	2.27	0.036
	2	2.475	2.138	-13.62	1.16	0.261
<i>Internal CO₂ concentration (ppm)</i>						
2.5	1	315	311	-1.24	0.32	0.175
	2	312	335	6.90	2.58	0.019
3.0	1	324	323	-0.23	0.09	0.930
	2	335	329	1.87	0.56	0.579

^aData collected 24 h after treatment under metal halide light providing a minimum of 1000 μmol·m⁻²·s⁻¹.

cut with a JB-4 microtome (Sorvall, Wilmington, Del.), mounted on slides, and stained with toluidine blue O (0.05% in water). From the treated plants, sections from 30 and 15 lesions on trifoliolate leaflets and 14 and nine lesions on primary leaves were examined in replicates 1 and 2, respectively. From the control plants, sections from 16 and nine pieces of trifoliolate leaflets and 14 and six pieces of primary leaves were examined in replicates 1 and 2, respectively.

Acidic fog effects on photosynthesis and stomatal resistance. Carbon dioxide assimilation rates were significantly ($P < 0.05$, paired and unpaired *t* tests) decreased by acidic fogs with pH values of 2.5 and 3.0 (Table 1). Over all three replicates, the decline in assimilation rate was not less than 33% for pH 2.5 fogs. Exposure to pH 3.0 acidic fogs caused assimilation rate reductions of at least 20%. Thus, exposure to acidic fogs clearly was detrimental.

Our observations of decreased CO₂ assimilation rate associated with acidic fog are not in agreement with previous reports of increases in photosynthetic rates of legumes treated with acidic rain (Ferenbaugh, 1976; Irving, 1979). However, these discrepancies are difficult to interpret because of differences in application technology, durations of exposure, and sulfate : nitrate ratios. Variation in plant responses between greenhouse environments and field systems almost certainly affected comparability (Chen and Goldstein, 1986). The length of time between exposure and recording of photosynthetic activity also would be of considerable significance, as several authors have reported that acidic precipitation may act as a foliar fertilizer (Bell, 1984; Irving, 1979; Tabatabai and Lafien, 1976).

In our study, some of the differences detected probably were due to the pretreatment, physiological standardization of the plants. No significant differences ($P > 0.05$) in CO₂ assimilation rates were detected when the plants were not standardized photosynthetically (Table 2, unpaired *t* test). In one case (pH 3.0, replicate 2), the CO₂ assimilation rate appeared to increase by >11%

following exposure to the acidic fog. This discrepancy indicates that interplant variation in *P. lunatus*, even among comparatively uniform plants grown concurrently in the greenhouse, may mask the effects of acidic precipitation on CO₂ assimilation. The general improvement in discrimination between CO₂ assimilation rates revealed by comparing the probability levels for the paired and unpaired *t* tests (Table 1) probably was influenced by the experiment design: the plants had been photosynthetically standardized before the treatments.

Initially, this apparent improvement in discrimination was attributed to the greater statistical separation power of the unpaired *t* test over the paired *t* test. However, additional analyses examining correlations between test and control plants showed no significant correlations ($P > 0.05$) for any of the physiological variables measured. Thus, the paired *t* test offered no statistical advantage over the unpaired *t* test in Expt. 1 (Snedecor and Cochran, 1978). Therefore, the standardized plants in Expt. 1 provided better statistical resolution than the unstandardized plants in Expt. 2 because of the reduction of overall variability in photosynthetic activity at the beginning of the experiments. The coefficient of variation in CO₂ assimilation for the standardized plants in Expt. 1 ranged from 9.15% to 13.6%, whereas that of the unstandardized plants in Expt. 2 ranged from 19.5% to 22.6%. The observed reduction in variability in Expt. 1 was an unintended result of the physiological pairing of the plants. Assuming a normal distribution for CO₂ assimilation rates for a plant population, the odds on selecting pairs of plants with similar assimilation rates are greatest near the mean assimilation rate. Thus, the pairing process itself was not critical; the same effect could be achieved by selecting plants with a coefficient of variation <10% for CO₂ assimilation rate.

Stomatal resistance increased significantly (Table 1, *t* test) in *P. lunatus* following exposure to acidic fogs. Over all three replicates, the increase in resistance was not less than 37% for pH 2.5 fogs and ranged as high

as 56%. Exposure to pH 3.0 acidic fogs caused stomatal resistance to increase by at least 27% (maximum = 34.9%). Physiologically pairing the plants before treatment again produced better discrimination between plants exposed to acidic and control fogs (Tables 1 and 2). In Expt. 2, where plants were not paired pretreatment, stomatal resistances were significantly increased only for replicate 1 of the pH 3.0 fog ($P < 0.036$, unpaired *t* test). In spite of a 30% increase in stomatal resistance for plants in replicate 1 of the pH 2.5 fog treatment (Table 2), the *t* value was not significant, further indicating that interplant variability in *P. lunatus* concealed potential treatment effects.

Internal CO₂ concentrations were not affected significantly by exposure to acidic fogs ($P > 0.05$, Table 1). Decreased CO₂ concentrations following treatment with pH 2.5 fogs only reached a maximum of 6.35% (minimum = 3.71%). There was a general trend for plants exposed to acidic fogs to have lower internal CO₂ concentrations than controls.

Acidic fog effects on leaf morphology. No new lesions >0.3 mm in diameter appeared in the delineated areas on control primary leaves, in contrast to more than 200 on treated primary leaves. Similarly, on the trifoliolates, only nine new lesions appeared on control leaves, in contrast to more than 1500 on treated leaves. The lesions on primary leaves tended to be much smaller than those on trifoliolates. Evans et al. (1977) also reported that acidic precipitation caused larger lesions on trifoliolate leaves than on primary leaves of *P. vulgaris*. The morphology of lesions in our study was similar for trifoliolate and primary leaves and between replicates; therefore, only a single generalized description follows.

Visibly damaged epidermal cells frequently were shrunken or obliterated in the area of the lesion (Fig. 1a-d, f). Visibly damaged palisade and spongy mesophyll cells often were shrunken and organelles were not visible. These mesophyll cells stained darkly and exhibited a "grainy" texture (Fig. 1) that indicated that their cellular structure had been destroyed and their cytoplasm had coagulated. Epidermal cells, which are mostly vacuole with little cytoplasm, usually did not exhibit this grainy appearance when damaged (Fig. 1b). Damage to upper epidermis usually was accompanied by damage to palisades (Fig. 1a-c); however, apparently healthy palisades occasionally were seen beneath damaged upper epidermal cells (Fig. 1d) and, conversely, damaged palisades occasionally were seen beneath an apparently intact upper epidermis (Fig. 1e and f). These latter two observations typically were seen at the margins of lesions. Damaged palisade cells beneath undamaged epidermis probably resulted from acid entering a leaf and moving laterally for short distances beneath the epidermis, destroying palisade cells but leaving the epidermis either intact or with no damage detectable by light microscopy. Alternatively, the acid could penetrate through the epidermis to the palisade layer without

necessarily causing the epidermal cells to collapse, thereby leaving no evidence detectable by light microscopy that epidermal damage had occurred.

Lignified xylem elements appeared to be relatively resistant to damage since intact-appearing xylem elements were commonly visible in areas where all of the surrounding mesophyll had been destroyed (Fig. 1 a-c). Evans et al. (1977) made similar observations for the effect of sulfate acid rain on *P. vulgaris*. While the xylem frequently remained intact within lesions, we cannot estimate how frequently the xylem tissue was destroyed because, once destroyed, it may no longer be identifiable as xylem. Functional xylem elements are dead conductive tubes and, therefore, would not be expected to exhibit the cytoplasmic coagulation seen in mesophyll cells. Additionally, the thick, lignified cell walls of xylem may be more resistant to acid than the relatively unlignified cell walls of mesophyll since lignin is not hydrolyzed by strong acids (Brauns, 1952).

Although xylem elements with intact cell walls were observed in the lesions, there was some effect on the xylem in replicate 2, where the lumen of the xylem elements frequently stained a uniform light to dark pink in treated leaves, but infrequently in control leaves. This observation suggests that something, perhaps coagulated xylem sap or hydrolyzed cellulose, could be occluding the xylem. Alternatively, the chemical constituency of the xylem sap may have changed with fog treatment and reacted differently with the histological fixative. Such staining was infrequently observed in either treated or control leaves in the first replicate.

Functional phloem sieve tubes are living cells with relatively unlignified walls and, therefore, are expected to be more susceptible to acid than xylem. Unfortunately, phloem is a delicate tissue that is difficult to fix well, thereby making it difficult to distinguish damaged from undamaged phloem. However, examination of phloem both inside and outside of many lesions gives the impression that phloem tissue is frequently collapsed in lesions where the adjacent xylem tissue is intact (Fig. 1 b and c). This difference suggests that when a lesion occurs over a vein, the area of the leaf distal to the lesion may be kept alive by water and nutrients supplied from the vein's undamaged xylem but would be unable to export photosynthates through the damaged phloem. This suggestion may offer at least a partial explanation as to why Jacobson et al. (1980) and Shriner and Johnson (1981) documented a change in photosynthate partitioning at the

expense of roots of other legumes damaged by acidic precipitation.

We suspect that both stomatal closure, as evidenced by increased resistance, and loss of healthy leaf area are responsible for the reduction in assimilation rate. However, Rubisco was not monitored and could reasonably be expected to have been impacted by the stressed plants exposed to acidic fogs. Additional experiments focusing on these variables will be necessary to document the specific mechanisms responsible for the observed effect.

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