Photosynthesis in Powdery Mildewed Sugar Beet Leaves

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ABSTRACT

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Net photosynthesis, dark respiration, and photorespiration were determined from rates of gas exchange by attached leaves of sugar beet (*Beta vulgaris*) infected with *Erysiphe polygoni*. Adaxial leaf surfaces were inoculated with conidia and the abaxial surfaces remained free of visible infection during the experimental period. At 6 days after inoculation, rates of net photosynthesis had measurably diminished and after 13 days had declined to less than half those of healthy leaves. Concomitantly, dark respiration increased and photorespiration decreased. Stomatal conductance was calculated independently for both the adaxial and abaxial leaf surfaces from their respective transpiration rates. For the mildewed adaxial surface, stomatal conductance was also calculated from adaxial CO_2 exchange rates and internal CO_2 concentration. The two methods gave similar values for the stomatal conductance of infected adaxial leaf surfaces, suggesting that the rate of water vapor loss by the fungus was small. Stomatal conductances on both the colonized and uncolonized sides of infected leaves declined during disease development. Mesophyll conductance to CO_2 was always much lower than stomatal conductance and was, therefore, of primary importance in limiting the rates of net photosynthesis by infected leaves. Under the light-saturated conditions that were used, the diminished photosynthetic capabilities of the mesophyll in infected leaves were not due to loss of chlorophyll or increased leaf reflectance.

Research workers studying powdery mildewed leaves have recently reported reduced rates of light-saturated net photosynthesis (3,10,13,21,22). These reductions cannot be explained by increases in dark respiration or photorespiration, but rather appear to reflect a reduction in the rate of CO_2 fixation (3,13,22). Under light-saturation, the rate of CO_2 fixation would generally be limited either by CO_2 supply, which is mediated primarily by stomatal conductance, or the carboxylation efficiency of the photosynthetic apparatus. The relative importance of these factors in contributing to the decline in photosynthetic rates of mildewed leaves has not been clearly established.

The factors potentially limiting photosynthesis in healthy leaves are readily evaluated by resolving total conductance to CO_2 uptake by the leaf into stomatal and mesophyll components. This requires an unambiguous measure of stomatal diffusive conductance; mesophyll conductance can then be determined as a residual term (15). Stomatal diffusive conductance is usually quantified in terms of water vapor loss by the leaf and then converted into a CO_2 conductance term (15). Unfortunately, mildew on the leaf surface contributes an unknown amount of moisture to the transpiration stream. Thus, stomatal conductance values based on transpiration data may not be reliable. Viscous flow porometry, a sensitive measure of stomatal aperture, has been used to evaluate stomatal conductance of mildewed leaves (3,22), but it is difficult to translate viscous flow conductance into the diffusive terms required for determining mesophyll conductance (16,23). Because of these difficulties, unambiguous estimates of mesophyll conductance are not available for mildew-infected leaves.

This paper presents the results of leaf-gas exchange experiments designed to determine the relative importance of stomatal and nonstomatal factors, including mesophyll conductance, in reducing net photosynthesis of sugar beet leaves infected with powdery mildew. A preliminary report of these results has been given (11).

MATERIALS AND METHODS

Sugar beet plants (*Beta vulgaris* L. 'USH 10') were grown from seed in sterilized soil in a controlled environment chamber under the following conditions: 98 $W \cdot m^{-2}$ of light in 400–700 nm wave band for 14 hr per day; day/night temperatures of 25/18 C; and day/night relative humidities of 65 ± 10%/75 ± 5%. Seven weeks after seeding, the youngest fully expanded leaf on each plant (either the 10th or 11th formed) was selected for inoculation and subsequent use in gas exchange experiments.

Leaves to be inoculated were inserted horizontally at the base of a 1.8-m-high settling chamber; only one leaf on each plant to be inoculated was within the chamber. Conidia of *Erysiphe polygoni* DC from previously infected leaves were introduced at the top of the chamber. Turbulence provided by air jets near the top of the

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chamber gave a thorough mixing of the spore suspension, which then settled, in the absence of crosscurrents, onto the leaves at the base of the enclosure. The inoculum was distributed uniformly at between 60 and 80 viable conidia per cm^2 of leaf area, as determined by counts of germinated conidia on eight glass slides that were interspersed among the leaves. Inoculated plants were returned to a growth chamber wherein conditions were the same as those under which the plants had been grown except that the irradiance was 90 $W \cdot m^{-2}$ in the 400–700 nm wave band. The light period was completed within 30–40 min after the plants were returned to the growth chamber; the one dark interval that immediately followed inoculation was extended to 18 hr with a relative humidity ≥80% during the first 10 hr of darkness. This procedure resulted in uniform mildew development on the adaxial surface and no colonization of the abaxial surface. Following completion of experiments involving a group of mildewed plants, the experiments were repeated with healthy plants that were grown under the same conditions described for inoculated plants.

On the evening prior to photosynthetic measurements, the leaf to be examined was enclosed within a highly ventilated Plexiglas chamber while remaining attached to the plant. The chamber was constructed after the design of Jarvis and Slatyer (17). Measurements were made on the 31 cm^2 of leaf area enclosed by the inner compartment, which had a total volume of 370 cm^3. The remainder of the leaf was within the confines of the outer compartment wherein conditions were similar to those in the inner compartment. The leaf blade divided the inner compartment into separate upper and lower halves of equal size, each supplied by an identical airstream of known CO_2 and water vapor concentrations. The two airstreams leaving the chamber were analyzed separately so gas exchange data could be obtained for each surface independently. To assure that mass flow through the amphistomatous leaf blade did not influence the exchange rates measured, the pressure differential across the leaf was maintained at less than 0.1 mm H_2O as measured with an electronic micromanometer. For all steady state measurements at light saturation, the following conditions impinged on the adaxial surface (upper half chamber): air temperature 28.8 ± 1.6 C; leaf to air vapor pressure gradient 7.6 ± 1.0 mm Hg; and CO_2 concentration 292 ± 6 ppm. The conditions for the abaxial surface (lower half chamber) were as follows: air temperature 26.8 ± 0.6 C; leaf to air vapor pressure gradient 7.2 ± 1.2 mm Hg; and CO_2 concentration 292 ± 8 ppm. Leaf temperature, measured with a fine wire copper-constantan thermocouple appressed to the abaxial leaf surface, was maintained at 27.4 ± 0.6 C. Light from two 500-W quartz iodine lamps filtered through 5 cm of water and a Schott KG2 glass filter (Schott Optical Glass, Inc., Duryea, PA 18642) provided a maximum photon flux density of 180 nanoeinsteins·cm^{-2}·s^{-1} which was determined to be 20% greater than that required for light saturation of net photosynthesis by sugar beet leaves.

Transpiration was determined from water vapor measurements with a dew-point hygrometer and CO_2 exchange was measured with a differentially calibrated infrared gas analyzer. For measurements to establish the relationship between light-saturated photosynthetic rate and external CO_2 concentration, the desired CO_2 levels were obtained by partial removal of CO_2 from the air prior to reaching the leaf chamber. Photorespiration was estimated by extrapolation of CO_2 dependence curves to zero CO_2 concentration and by taking the difference between CO_2 fixation rates in 1 and 21% O_2 (20). Dark respiration was measured during the night preceeding photosynthetic measurements with leaf temperatures of 24.9 ± 1.1 and a CO_2 concentration of 320 ± 2 ppm at both leaf surfaces. Measurements of photosynthesis, photorespiration, and leaf conductance were completed during a 10-hr period on the following day.

Standard procedures, which rely on water vapor exchange data, were used to evaluate the diffusive pathway for CO_2 uptake by the leaf (15). Conductance to water vapor was obtained from the equation: $E=(C_w - C_a)/(1/L_a' + 1/L_1')$ in which $E(\mu g \cdot cm^{-2} \cdot s^{-1})$ is the transpiration rate; C_w and C_a ($\mu g \cdot cm^{-3}$) are, respectively, the water vapor concentrations at the surface of the mesophyll cell walls and in the bulk air; L_a' ($cm \cdot s^{-1}$) is the boundary layer conductance to water vapor transfer and L_1' ($cm \cdot s^{-1}$) is the leaf conductance associated with stomatal and cuticular pathways of transpiration. The value of C_w was taken as the saturation water vapor concentration at the temperature of the leaf. L_a' was determined to be 3.57 ($cm \cdot s^{-1}$) for both the upper and lower chambers, by using a wet filter paper replica of the leaf.

The total conductance of the CO_2 pathway (L_t) from ambient air to the sites of carboxylation, for each side of the leaf, was taken as the slope of the line relating rate of CO_2 uptake to the ambient CO_2 concentration, measured under light saturating and CO_2-limiting conditions. The intracellular or mesophyll conductance (L_m) was then deduced as follows: $1/L_m = 1/L_t - 1/L_1$, in which $L_1 = 0.64\, L_1'$ to correct for the different diffusion coefficients for CO_2 and H_2O in air (15). Determined in this way, mesophyll conductance is a residual term pertaining to that segment of the pathway that remains when the stomatal component, determined from water vapor exchange data, has been subtracted.

Estimates of stomatal conductance to CO_2 uptake from transpiration data are premised on the assumption that all moisture contributed to the transpiration stream passes through the stomatal pores (15). For the adaxial surface of mildewed leaves, the measured rate of transpiration includes an unknown amount of moisture originating from fungal mycelium and conidia on the leaf surface. Thus, the accuracy of the calculated stomatal conductance values for mildewed leaf surfaces is in doubt. For this reason, stomatal conductances of the mildewed adaxial leaf surfaces were also calculated by an alternative method, the parameters of which are diagrammed in Fig. 1. First, the CO_2 concentration in the intercellular air spaces, $[CO_2]_i$, was calculated as $[CO_2]_i = [CO_2]_a^{ab} - (J_{CO_2}^{ab} / L_1^{ab})$ in which $J_{CO_2}^{ab}$ is the flux of CO_2 into the opposite (abaxial) side of the leaf, $[CO_2]_a^{ab}$ is the concentration of CO_2 in the

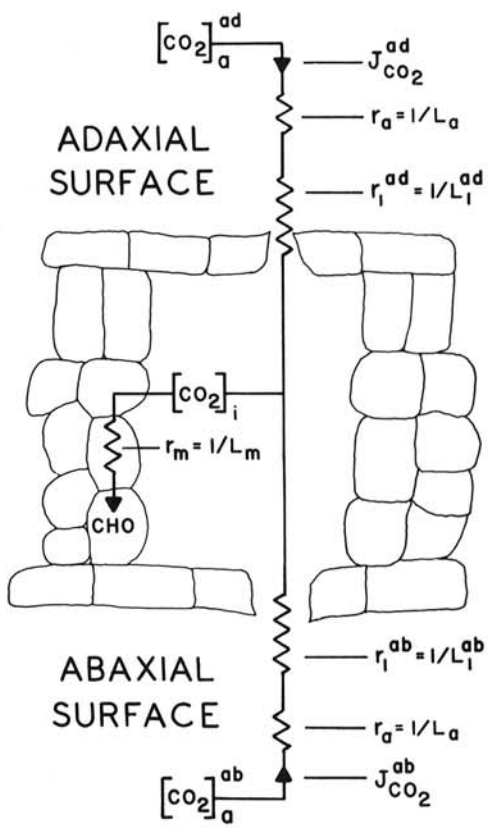

Fig. 1. A diagrammatic cross section of an amphistomatous sugar beet leaf showing the relationship between net inward CO_2 flux ($J_{CO_2}^{ad}$, $J_{CO_2}^{ab}$), boundary layer conductance (L_a), stomatal conductances (L_1^{ad}, L_1^{ab}), mesophyll conductance (L_m), ambient CO_2 concentrations ($[CO_2]_a^{ad}$, $[CO_2]_a^{ab}$), and internal CO_2 concentration ($[CO_2]_i$). The resistances (r_1^{ad}, r_1^{ab}, r_m, and r_a) are the reciprocals of the corresponding conductances.

ambient air surrounding the abaxial surface, and L_1^{ab} is the abaxial conductance to the diffusive transfer of CO_2 from the ambient air into the leaf. Then, by assuming that the internal CO_2 concentration calculated for the abaxial side of the leaf is applicable to the adaxial side, stomatal conductance to CO_2 uptake on the adaxial surface (L_1^{ad}) was obtained from the equation $1/L_1^{ad} = [CO_2]_a^{ad} - [CO_2]_i / J_{CO_2}^{ad} - 1/L_a$ in which $J_{CO_2}^{ad}$ is the flux of CO_2 into the adaxial side of the leaf, $[CO_2]_a^{ad}$ is the concentration of CO_2 in the ambient air above the leaf, and $L_a = 0.74\ L_a'$, which adjusts the boundary layer component for the difference in diffusion coefficients of CO_2 and H_2O within the boundary layer (15).

To assess the extent to which mildew on the leaf surface increased the reflectance of photosynthetically active radiation, disks were removed from diseased and healthy leaves for absorptance determinations with an Ulbricht integrating sphere internally coated with Eastman 6080 white reflectance coating (Eastman Kodak Co., Rochester, NY 14650). Theory and description of the Ulbricht sphere have been discussed by Rabideau et al (24). Absorptances were measured by directing light from a 2.5-kW xenon arc lamp into the sphere and using a quantum sensor to measure light reflected from leaf disks and the reflectance standard (a flat disk coated with Eastman 6080). Total chlorophyll determinations were made for each leaf by homogenizing 16 cm^2 of interveinal leaf tissue in 80% acetone. The extract was filtered and then assayed as described by Arnon (1).

RESULTS

Three days after leaves were inoculated the adaxial surface had a uniform cover of *E. polygoni* mycelium; microscopic examination of leaves at this time revealed ≥95% of the 1-mm-square fields observed contained fungal hyphae. Sporulation was evident at 6 days, and by 13 days after inoculation a dense, powdery mass of conidia was present on the adaxial surface. The abaxial leaf surface remained free of visible fungal growth during the experimental period. There was no chlorosis or necrosis of infected leaves.

Net photosynthesis declined steadily with time after inoculation (Fig. 2A), and dark respiration was somewhat elevated in diseased leaves, relative to uninoculated controls (Fig. 2B). In contrast to dark respiration, rates of photorespiration actually declined as disease progressed and, therefore, could not have contributed to the decline in net photosynthesis. Photorespiratory rates (Fig. 2B) were obtained by extrapolation of photosynthetic CO_2 dependence curves to zero CO_2 concentration. Similar results were obtained when photorespiration was taken as the difference between the CO_2 fixation rate in 21 and 1% O_2 (20).

The rate of photosynthesis measured separately for the adaxial surface of the leaf declined almost linearly with time after inoculation (Fig. 3A), whereas the abaxial surface showed enhanced photosynthesis at 3 days after inoculation and a steady decline thereafter (Fig. 3B). For both sides of the leaf, changes in CO_2 conductance, as calculated independently for each surface from their respective water vapor and CO_2 exchange rates, paralled the changes in photosynthetic rate. Altered mesophyll and stomatal conductances both contributed to the decline in photosynthesis during disease development but the data in Fig. 3 clearly show that mesophyll conductance, the lowest of two conductances in series, had proportionately more influence on the total conductance to CO_2 uptake. For example, the total conductance to CO_2 uptake for the abaxial side of a diseased leaf at eight days after inoculation was 0.085 $cm \cdot s^{-1}$, which is 46% of the value for the abaxial side of a comparable healthy leaf. If abaxial stomatal conductance is

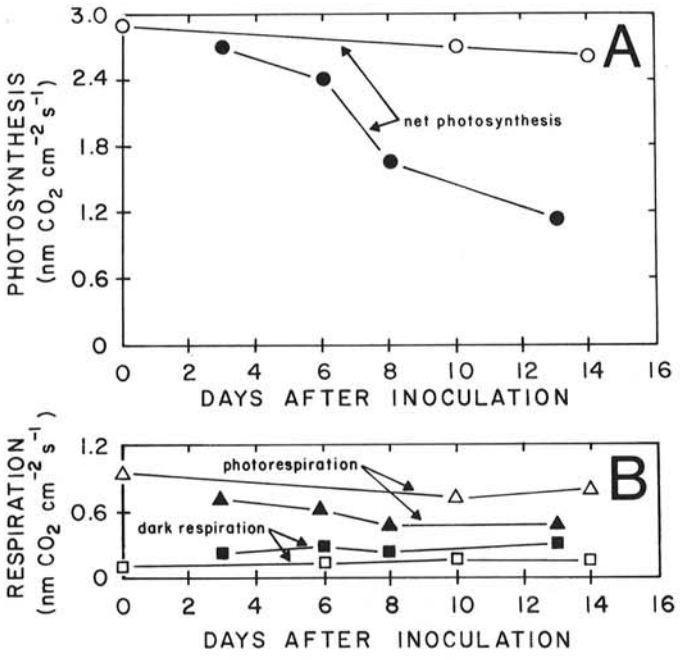

Fig. 2. A, Net photosynthesis, **B**, photorespiration, and **B**, dark respiration rates of healthy (open symbols) and mildewed sugar beet leaves (closed symbols) plotted as functions of the time after adaxial surfaces of mildewed leaves were inoculated with conidia of *Erysiphe polygoni*. Rates are the summation of the nanomoles of CO_2 fixed or respired per square centimer of adaxial and abaxial leaf surface per second.

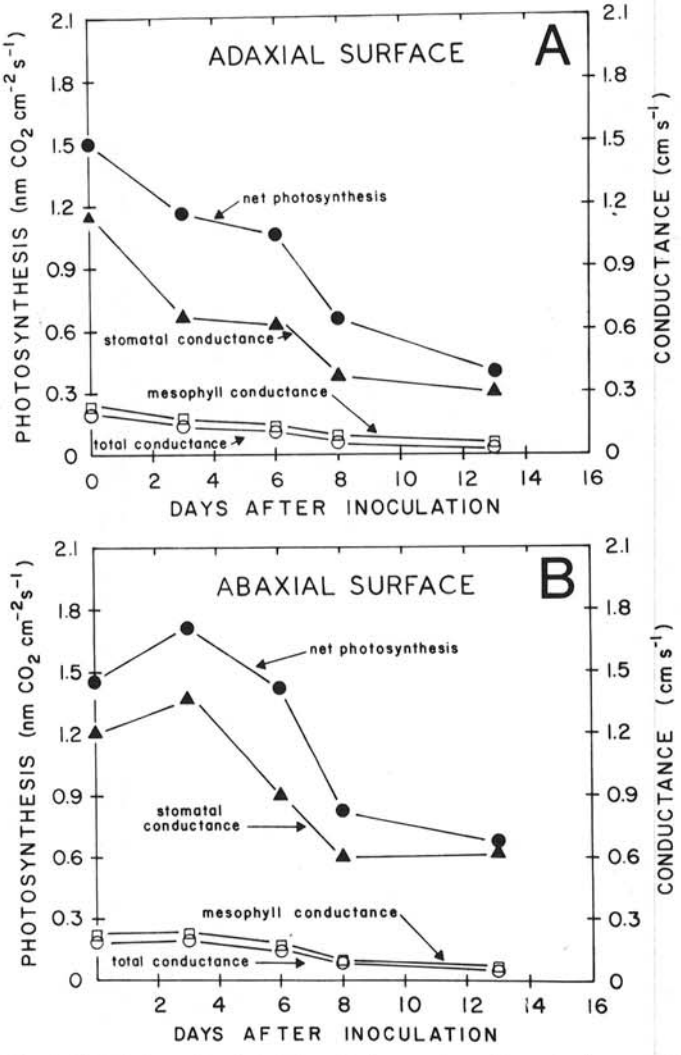

Fig. 3. Net photosynthesis, total conductance, stomatal conductance, and mesophyll conductance measured separately for the **A**, adaxial and **B**, abaxial surfaces of mildewed sugar beet leaves, plotted as functions of time after inoculation of the adaxial surfaces with conidia of *Erysiphe polygoni*. Stomatal conductances to CO_2 were calculated independently for each surface from their respective rates of water vapor loss. Total conductance was estimated separately for the two leaf surfaces from the CO_2 dependence of photosynthesis, and the mesophyll conductance apparent at each surface was obtained as the difference between the total and stomatal resistances.

increased from 0.60 to 1.25 cm·sec^{-1}, a representative value for a healthy leaf, total conductance would be increased to only 0.092 cm·s^{-1} or 49% of the value for a healthy leaf. Furthermore, $[CO_2]_i$ is not decreased as a result of infection with *E. polygoni* (Table 1), indicating that CO_2 uptake is limited by the inherent capacity of the mesophyll to fix CO_2 and not by stomatal conductance. As data in Fig. 2A would suggest, the photosynthetic rates and conductances measured separately for both surfaces of healthy leaves change very little from those shown for a healthy leaf at day zero in Fig. 3. The results in Figs. 2 and 3 were obtained by using one plant for each day of measurement. A repeat of the gas exchange measurements on a separate group of plants over the same time period gave almost identical results for both healthy and diseased leaves.

Stomatal conductance values for adaxial leaf surfaces, which were calculated from the internal CO_2 concentration deduced from gas exchange data for the abaxial surface, are shown in Table 1. These values differ from those obtained by using rates of water vapor flux from the adaxial surface by no more than 17%. Regression of one set of values on the other gives an r^2 value of 0.98. Thus, the stomatal and mesophyll components of conductance calculated from water vapor exchange rates and shown for CO_2 uptake by the adaxial leaf surface in Fig. 3A appear to be reasonably accurate. It seemed possible that decreased stomatal conductance might result from the higher internal CO_2 concentrations in diseased leaves (Table 1) and could therefore be a secondary effect of lowered rates of CO_2 assimilation (25). However, reducing CO_2 concentration within the leaf by partial or complete removal of CO_2 from the airstreams entering the chamber did not increase the stomatal conductances of diseased leaves.

Leaf-water potentials were determined with a thermocouple psychrometer at the conclusion of gas exchange measurements on each leaf. Water potentials ranged from −9.6 to −11.9 bars and there was no evidence of water stress in either diseased or healthy leaves. In fact, under the conditions used there was no significant difference in water potential between mildew-infected and healthy sugar beet leaves.

Light absorptance and total chlorophyll concentration decreased slightly as the disease developed. At zero and 14 days after inoculation, the absorptance of healthy leaves was 0.926 and 0.920, respectively; whereas at 7, 14, and 18 days after inoculation the absorptance of infected leaves was 0.898, 0.885, and 0.879, respectively. Healthy leaves had 45 to 48 μg of chlorophyll per square centimeter of leaf area, whereas infected leaves had 42, 40, and 39 μg chlorophyll per square centimeter at 7, 14, and 18 days after inoculation.

DISCUSSION

Decreased mesophyll conductance appears to be the chief mitigating factor in the progressive decline of net photosynthesis in mildewed sugar beet leaves. Mildew was not present on the abaxial surface so the total conductance to CO_2 of this surface was readily resolved into its stomatal and mesophyll components. While abaxial stomatal conductance was progressively reduced during mildew development (Fig. 3B), the mesophyll component was invariably much smaller and was the primary determinant of total CO_2 conductance. Since an effect on mesophyll conductance was evident on the abaxial side of the leaf while the fungus was restricted to the adaxial surface (and underlying epidermal cells), it seems inevitable that such an effect is operative throughout the diseased leaf.

The conductance measurements for the adaxial leaf surface also support the conclusion that mildew development greatly reduces the photosynthetic competence of mesophyll cells. However, fungal growth on the adaxial surface renders the resolution of its total conductance into stomatal and mesophyll components less certain. Previous investigators have physically removed the mycelium of the powdery mildew pathogen to eliminate its confounding effect on stomatal conductance measurements (3,22). Unfortunately, the physical abrasion required to tear the superficial hyphae from the subtending haustoria could have undesirable effects on stomatal function. For example, in one study comparable abrasion of healthy leaves reduced their transpiration rate (22) suggesting partial stomatal closure. Ayres (3) found that the removal of *E. polygoni* mycelium increased transpiration in infected pea leaves and concluded that the increase resulted from the elimination of a boundary layer effect imposed by the fungus. Other explanations are possible. Damaged haustoria may serve as new high conductance pathways for water vapor loss, and direct damage to the host cuticle could also have increased leaf conductance to water vapor loss. Thus, removal of fungal mycelium from mildewed leaves would not seem to yield an unambiguous measure of their stomatal conductance.

We have attempted to avoid the complicating influence of powdery mildew mycelium by using gas exchange data from the uncolonized abaxial surface to verify measures of stomatal conductance on the colonized adaxial surface (Fig. 1). This approach is subject to error to the extent that the internal CO_2 concentration determined from the abaxial side of the leaf differs from that in the air spaces more near the adaxial side of the leaf (18). Sugar beet leaves, however, are highly isolateral (2,5,12), and even in mildewed leaves rates of CO_2 uptake did not differ greatly between the two surfaces (Fig. 3). Therefore it is unlikely that a substantial gradient in CO_2 concentration exists within the mesophyll air spaces of the leaf. For healthy leaves there is good agreement between stomatal conductances calculated from their adaxial water vapor flux or from their adaxial CO_2 flux in combination with an internal CO_2 concentration deduced from abaxial surface gas exchange rates. That two such divergent procedures gave similar values in mildewed leaves (Table 1) is somewhat more surprising. It could mean there are compensating errors in the two techniques, but this seems unlikely in view of the results obtained with healthy leaves. An alternative explanation is that the fungal tissue loses a negligible amount of water vapor relative to the leaf (27). If this is the case, the stomatal conductance values based on transpiration data reported here and previously (22) for powdery mildewed leaves were not greatly affected by the mycelium on the leaf surface. Such values still include a boundary

TABLE 1. Stomatal conductances for the adaxial surface of sugar beet leaves infected with powdery mildew, calculated by two different methods, and internal CO_2 concentrations determined for the same leaves

		Adaxial stomatal conductance to CO_2		
Days after inoculation	Treatment	Calculated from adaxial water vapor flux[a] (cm·s^{-1})	Calculated from adaxial CO_2 flux and internal CO_2 concentration[b] (cm·s^{-1})	Internal CO_2 concentration[b] (nm·cm^{-3})
0	Healthy	1.15	1.34	9.59
3	Infected	0.68	0.63	9.79
6	Infected	0.63	0.74	10.14
8	Infected	0.40	0.40	9.97
13	Infected	0.32	0.34	10.81
18	Healthy	1.31	1.47	9.95

[a] Calculated from water vapor exchange data for the adaxial surface and converted to a CO_2 conductance term.
[b] Calculated from water vapor and CO_2 exchange data for the abaxial surface, and in the case of the adaxial stomatal conductance, the adaxial CO_2 flux.

layer effect that is not readily quantified; hence they do not necessarily reflect changes in stomatal aperture. However, based on studies of leaf hair effects on boundary layer conductance, the boundary layer effect resulting from mycelium on the leaf surface is probably a minor component of the decrease in leaf conductance (9). In any case our reported values of stomatal conductance appear to provide a valid measure of conductance to the flux of CO_2 from the ambient air to the internal air spaces within the leaf. It is important to note that even if the mycelium transpired sufficiently to cause stomatal conductance on the adaxial surface to be overestimated by as much as 20 or even 30%, stomatal conductance would still have a very small effect on the total conductance. Therefore, our conclusion about the overriding importance of mesophyll conductance in limiting photosynthetic rates of diseased leaves would remain unaffected. The lack of an important stomatal effect on photosynthesis is underscored by the fact that CO_2 concentration is actually somewhat higher in mildewed leaves compared with healthy controls (Table 1).

Although it does not have a major impact on photosynthesis, a measurable decrease in stomatal conductance does occur with mildew development and, at least on the abaxial surface, it must reflect decreased stomatal aperture. Reductions in stomatal aperture have been reported for mildewed leaves of other hosts (3,4,13). The underlying cause is not known but, at least for mildewed sugar beets, it apparently does not result from elevated CO_2 levels within the leaf.

As determined from leaf-gas exchange measurements, mesophyll conductance is a function of both the physical transport of CO_2 in the liquid phase from the surface of the mesophyll cell walls to the sites of carboxylation and the efficiency of the fixation process itself (15). The former is a purely physical component that would not be expected to differ substantially between diseased and healthy leaves (12,15). Therefore, disease-induced reductions in mesophyll conductance are probably the result of metabolic alterations that occur within the chloroplast. Such alterations may include decreases in the activity of enzymes catalyzing the reductive pentose phosphate cycle, depletion of important metabolites, or both. It has been suggested that the effect of powdery mildew infection on net photosynthesis of its host results primarily from diminished capacity of mesophyll tissue to fix CO_2 (13,21,22), and evidence has been presented (21) for an effect of the disease on light-limited reactions in chloroplasts isolated from mildewed sugar beet leaves at an advanced stage of infection (30 days after inoculation). Ours is the first experimental demonstration of an effect of this disease on mesophyll conductance that can explain the observed reduction in light-saturated rates of net photosynthesis. Similar findings have been reported for virus and vascular wilt diseases (8,12).

Magyarosy et al (21) found no change in the chlorophyll content of mildewed sugar beet leaves. Our data show a slight reduction in chlorophyll content as early as 7 days after inoculation but not enough to cause any visible chlorosis even at 18 days after inoculation. Chlorophyll losses of the magnitude reported here would not be expected to affect the efficiency of light utilization (26).

The decrease in absorptance of mildewed leaves will reduce the amount of photosynthetically active radiation reaching the photosynthetic tissue within the leaf. However, reduced absorptance did not contribute to the discrepancy in photosynthetic rates between diseased and healthy leaves reported here because light saturation was established for each leaf under study. Absorptance changes of this magnitude probably would have no significant impact on photosynthetic rates of fully exposed leaves of field-grown plants, but for shaded leaves, operating near the light-compensation point, reduced absorptance may be important (7).

The gradual increase in dark respiration of diseased leaves makes a negligible contribution to the reduction in net photosynthesis (Fig. 2), a result that is consistent with results reported for powdery mildews on other hosts (6,22). Declining rates of photorespiration (Fig. 2B) in mildewed sugar beet leaves are in agreement with a recent report on photorespiration in mildewed oak leaves (13). In contrast, Ayres (3) reported a transient increase in photorespiration of mildewed peas. Declining rates of photorespiration, as we have reported, suggest that reduced photosynthetic efficiency does not result from altered affinity of ribulose bisphosphate carboxylase/oxygenase for O_2 relative to CO_2. This conclusion was also arrived at by Mignucci and Boyer (22) regarding mildewed soybeans.

Obviously, infection with powdery mildew will be a detriment to the productivity of sugar beets. Diseased leaves will have sharply reduced maximum (light-saturated) photosynthetic rates. Of course, the effect could be less dramatic when infection is light and discrete colonies are formed. Under these circumstances, healthy tissue may show enhanced photosynthetic rates that could partially offset the lower rates in infected areas. In the present study, a stimulation of photosynthetic CO_2 uptake was recorded for the abaxial surface at 3 days after inoculation as a result of higher total conductance to CO_2 for this surface (Fig. 3B). Increased rates of photosynthesis have been reported for the early stages of mildew and rust infections (13,19,28). In addition to the likely difference between partially and entirely colonized leaves, mildew develops most extensively on shaded leaves in the field, so the reductions in light-saturated photosynthesis reported here are not expected to cause equally large reductions in yield (14).

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