Influence of CO_2 Uptake of Barley Leaves on Incubation Period of Powdery Mildew Under Different Light Intensities

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ABSTRACT

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Uptake of CO_2 was measured on both sides of barley leaves following inoculation of the leaves with *Erysiphe graminis* f. sp. *hordei*. The CO_2 uptake increased during infection whereas it decreased during incubation and sporulation. Disease development had little influence on the gas exchange through the upper epidermis since 82% of the CO_2 passed through the lower epidermis in all treatments. However, a positive correlation (r = 0.992) was found between light intensities, length of incubation period, and CO_2 uptake by infected leaves.

Additional key words: host-parasite relationship, physiology, epidemiology.

Temperature is a major climatic factor affecting incubation periods in plant diseases. However, it is possible that in diseases caused by obligate parasites light intensity also may influence the incubation period (2, 3). Such an effect of light could be explained by an increase in leaf temperature due to radiation and/or by the light-dependent increase in the CO_2 uptake of the host plant. In the latter case increased photosynthesis could provide a higher nutrient level in the infected tissue and thereby ameliorate interference of the parasite with host metabolism, and rate of lesion formation. We studied the effect of CO_2 assimilation on the incubation period (time between inoculation and colony appearance) of *Erysiphe graminis* DC. f. sp. *hordei* Marchal on barley (*Hordeum vulgare* L.) in growth chambers in which the leaf temperatures did not differ significantly from the air temperatures (5). *Erysiphe graminis* f. sp. *hordei* affects mainly the upper epidermis, therefore the experiments should clarify whether the gas exchange of the upper leaf surface changes during the disease development and whether a higher CO_2 assimilation can prolong the incubation period.

MATERIAL AND METHODS

Test plants belonged to the spring barley cultivar Firlbecks Union. The inoculum was obtained from mildewed plants collected in a field with a population of *E. graminis* f. sp. *hordei* consisting mainly of the virulence (Vg) to which the cultivar is highly susceptible. The test plants were raised in growth chambers at 22 ± 0.5 C, 70 ± 1% RH, and a light intensity of 0.28 cal·cm^{-2}·min^{-1} (= 38,000 lx at plant height), and a photoperiod of 12 hr. The light source of the growth chambers was equipped with six HPI-lamps (Philips – 126647, 400 W). Seven-day-old plants received an average spore load of 286 ± 43 conidia cm^{-2} in an inoculation tower (4); 75 ± 9 of the conidia landing on the leaf surfaces formed secondary hyphae [as checked with the gelatin-stripping-method (13)]. In an infrared gas analyser (type URAS 2T, Hartmann & Braun AG, Frankfurt), uptake of CO_2 was measured periodically on both sides of detached leaves in gas-changing-cuvettes inserted in a thermostatic water bath beginning at the time of inoculation (6). The climatic conditions in the gas-changing-cuvettes corresponded to the growth conditions of the experimental plants mentioned above except light intensity.

Carbon dioxide was introduced into the measuring air by a compressed-air-unit; the concentration varied from 0.0325 to 0.0332%. The infrared gas analyser was calibrated with standardized gas. During the measurements the system was illuminated with a PRADO-UNIVERSAL projector equipped with a series of grey filters. The grey filters change the light intensity only and not the light quality. The light source of the projector was a tungsten halogen lamp (Philips - 7748, 24 V, 250 W), with a light quality different from that in the growth chambers.

The CO_2 exchange of the infected leaves was measured at five light intensities (Fig. 1, 2, 3). These measurements were done at infection, incubation, and sporulation, respectively, which corresponded approximately to 45 to 60, 70 to 85, and 140 to 155 hr after inoculation. These three periods seem to be important stages in the development of the parasite (4). Simultaneously, CO_2 exchange measurements were made with noninoculated plants of the same age. All treatments were done in four replicates, and are expressed as means with standard deviations.

RESULTS

Figures 1, 2, and 3 show the relation between light intensity and CO_2 exchange of healthy and infected leaves. The values above the zero line represent the

apparent CO_2 exchange of the detached leaves; those below the CO_2 release. The data for the dark respiration are presented in Table 1.

During infection, CO_2 assimilation (apparent CO_2 uptake + dark respiration) was 5-10% greater with infected than with healthy leaves at all light intensities (Fig. 1). The dark respiration during that period exceeded the control (Table 1.) Eighty percent of the total CO_2 was taken up through the lower epidermis. These differences were not due to more stomata on the lower surface; 2,926 and 2,497 stomata cm^{-2} were found on the upper and lower leaf surfaces, respectively.

During incubation the total CO_2 assimilation (apparent CO_2 uptake + dark respiration) by infected leaves reached only about 80-90% that of the healthy leaves (Fig. 2), but dark respiration of the infected leaves was nearly doubled (Table 1). Again these differences became greater with increasing light intensity. A further decrease of CO_2 uptake by the infected leaves (64-75% of the control) occurred during sporulation (Fig. 3). The dark respiration during that stage was 4.5 times higher than that of the controls (Table 1).

Figure 4 shows agreement between the incubation periods derived from data of a previous study (5) and the total CO_2 exchange by the infected leaves in the present study (Fig. 2). To determine whether a correlation existed between the incubation period and the CO_2 uptake, five points at the same light intensities were taken from both curves (Fig. 4) and plotted against each other (Fig. 5). The relation was a highly correlated (r = 0.992) regression, y =

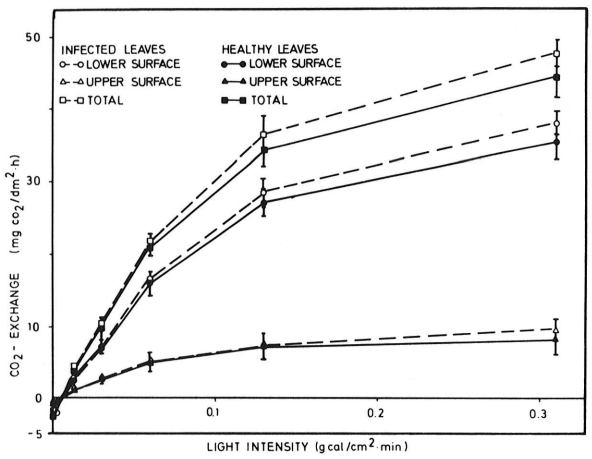

Fig. 1. The CO_2 exchange of barley leaves infected with *Erysiphe graminis* f. sp. *hordei* during the infection period (45-60 hr after inoculation) at 22 C, 70 % relative humidity, and different light intensities.

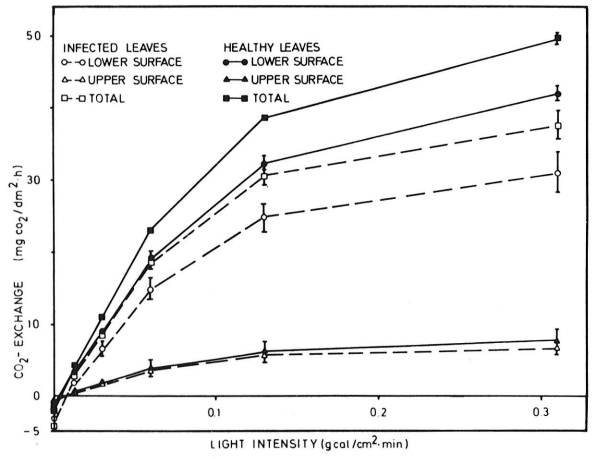

Fig. 2. The CO_2 exchange of barley leaves infected with *Erysiphe graminis* f. sp. *hordei* during incubation (70-85 hr after inoculation) at 22 C, 70 % relative humidity, and different light intensities.

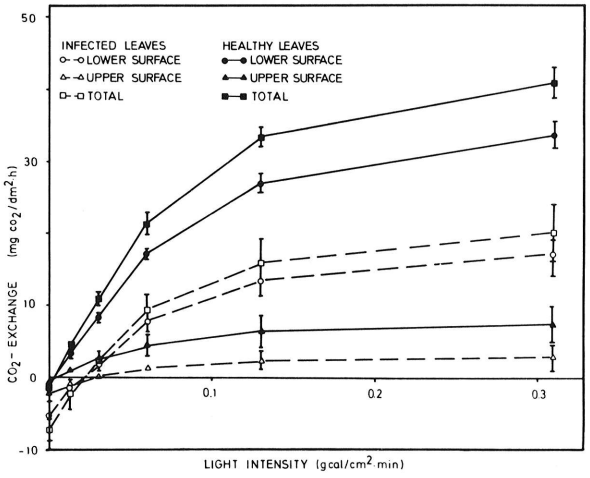

Fig. 3. The CO_2 exchange of barley leaves infected with *Erysiphe graminis* f. sp. *hordei* during sporulation (140-155 hr after inoculation) at 22 C, 70 % relative humidity, and different light intensities.

TABLE 1. Dark respiration of detached barley leaves (mg CO_2 $dm^{-2} \cdot hr^{-1}$) infected with *Erysiphe graminis* f. sp. *hordei*

Time after inoculation in hours	Healthy leaves			Infected leaves		
	Lower surface	Upper surface	Total	Lower surface	Upper surface	Total
45-60	-1.7±0.1	-0.5±0.2	-2.2±0.1	-2.0±0.3	-0.7±0.2	-2.7±0.5
70-85	-1.5±0.2	-0.6±0.1	-2.2±0.2	-3.3±0.4	-0.9±0.4	-4.1±0.8
140-155	-1.3±0.4	-0.3±0.3	-1.6±0.4	-5.3±0.5	-1.9±1.3	-7.2±1.5

51.91 + 0.89 x, where y is the incubation period and x is the rate of CO_2 assimilation.

DISCUSSION

The general course of pathogenesis by obligate parasites and their physiological effects on the host has been investigated elsewhere (1, 8, 9, 10, 11, 12, 14). Our results confirm that during incubation and sporulation, CO_2 uptake (i.e, photosynthesis) decreases, whereas respiration increases (Fig. 2, 3; Table 1). However, during the infection process (45-60 hr after inoculation we detected a slight increase in CO_2 uptake at a CO_2 concentration of 0.033 %. Our work in progress will have to show whether this result, which conflicts with other reports (8, 10), is consistent or whether it reflects the use of different techniques of measurement and inoculation.

The results in Fig. 4 and 5 suggest that light intensities within a certain range may influence the incubation period of obligate parasites via the metabolism of the host; latent period of *E. graminis* f. sp. *hordei* lasts 102 hr at light intensities of 0.05 to 0.28 cal · cm^{-2} · min^{-1} and 22 C and 108 hr at 0.34 cal · cm^{-2} · min^{-1} (5). At 22 C and light intensities above 0.28 cal · cm^{-2} · min^{-1} changes in the metabolism of the host or the parasite seem to delay the development of the fungus due to a higher leaf temperature (5). At light intensities lower than 0.05 cal · cm^{-2} · min^{-1} the nutrient supply may no longer be adequate for the fungus owing to a reduced photosynthesis in the host, which could result in a longer latent period.

Our experiments were based on the assumption that the pathway for the transport of CO_2 through the upper epidermis could be changed by the infection apparatus of the fungus. This in turn could alter the CO_2 exchange rate of both surfaces of the infected barley leaf which might result in a change of diffusion resistance of the epidermis. A decline in the diffusion resistance could be caused by a local destruction of the outer epidermal cell walls. Alternatively, an increase in the diffusion resistance following fungal infection could occur due to loss of turgor of the injured epidermal cells. Both hypotheses seem unlikely since during the course of disease development (infection, incubation, sporulation) 82% of the total CO_2 exchange was provided by the stomata of the lower leaf surface which constitute only 46% of the total stomata.

The guard cells of the stomatal apparatus of both leaf surfaces can react very differently (7). In a field experiment, temperature measurements at both leaf surfaces of barley show that the temperature of the upper epidermis can exceed that of the lower epidermis by about + 4 C at a high light intensity of 1 cal · cm^{-2} · min^{-1} (H. J. Aust, *unpublished*). The temperature increase and the reduction of the gas exchange (Fig. 1, 2, 3) at the upper leaf surface could be caused by a reduction of the stomatal aperture. This would lead to a reduction in the water loss of the light-oriented upper epidermis and would provide a better control of the water relations through the lower surface of the barley leaf. The leaves of the Gramineae seem to be adapted very well to their habitat in relation to the rate of the gas exchange of both leaf surfaces. For instance, corn leaves at different levels of leaf insertion exhibit very different CO_2 exchange patterns. The partitioning of the CO_2 exchange of the lower epidermis increases with increasing insertion height of the leaf due to water stress (6). Rice leaves on the other hand exchange more than 60% of their CO_2 through the light-oriented upper leaf surface which contains only 42% of the total stomata (Domes and Leihner, *unpublished*). Since rice plants were cultivated in flooded plots with abundant water supply there seems to be no necessity for them to reduce the gas exchange at the light-oriented upper leaf surface.

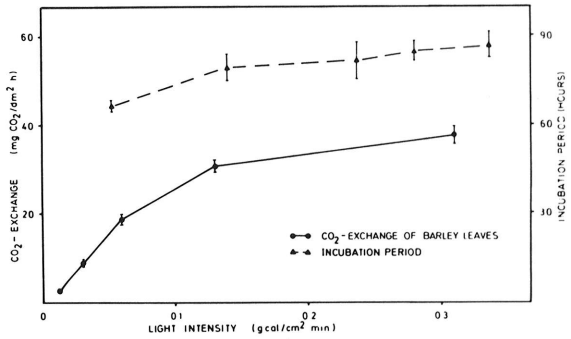

Fig. 4. The CO_2 exchange of barley leaves infected with *Erysiphe graminis* f. sp. *hordei* and incubation periods of the barley powdery mildew in relation to the light intensity at 22 C.

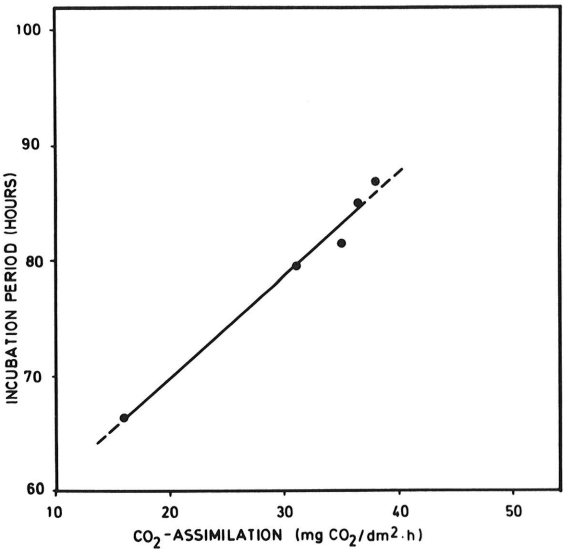

Fig. 5. Incubation periods of *Erysiphe graminis* f. sp. *hordei* in relation to the CO_2 assimilation of barley leaves infected with *Erysiphe graminis* f. sp. *hordei* during the incubation period at 22 C.

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