Effects of Foliar Diseases on Gas Exchange Processes: A Comparative Study

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ABSTRACT

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The effects of 10 different foliar diseases on the photosynthetic and transpirational activities of five annual and three perennial crops were examined under field conditions. The following pathosystems were investigated: leaf rust, powdery mildew, and Septoria tritici blotch of wheat; rust of corn; downy mildew of cucumber; Alternaria leaf spot of cotton; powdery mildew of pepper; Pestalotia of mango; powdery mildew of peach; and powdery mildew of grapes. Visual estimates of infection do not always indicate adequately the effect of a pathogen on these physiological processes. Three different patterns of host response were observed in diseased leaf area relative to disease-free leaf area. The decrease in rate of photosynthesis or transpiration was a) proportional, b) proportionally greater, or c) proportionally smaller than the corresponding reduction of healthy leaf area due to disease. Host responses were not always related to the systematic group of either the host or the pathogen. The pattern of responses and the amount of reduction in photosynthesis and/or transpiration rates were, however, related to the type of trophic relationships. This article provides regression models that may be used for incorporating the effects of various foliar diseases to crop growth simulators.

Knowledge of the effect of pests and diseases on host physiological processes has become increasingly important with the development of integrated pest management. A useful means of investigating these effects is provided by process-oriented models that describe crop growth and partitioning of photosynthate assimilates on the basis of environmental inputs (4,16). Incorporating disease effects to crop models has been discussed from the physiological point of view. Boote et al (4) grouped pest effects on plant growth into seven categories: tissue consumers, leaf senescence accelerators, stand reducers, light stealers, photosynthetic rate reducers, assimilate sappers, and turgor reducers. Johnson (15) divided these pest effects into two large groups, characterized by major effects on solar radiation interception (the first four) and major effects on relative use efficiency (the last three). Since photosynthesis is the biological process that leads to yield accumulation, and because the water status of the crop markedly affects photosynthesis, carbon metabolism and water relations are critical areas of concern in understanding the effects of disease on plants (17).

Much is known about the effects of pathogens on photosynthesis and transpiration. A reduction in net photosynthesis following infection has been shown by several authors in a range of pathosystems. In some pathosystems, photosynthesis was initially stimulated or not affected but later decreased (9,17,18,20–22). Reductions in photosynthetic activity are caused by a decrease in the photosynthesizing leaf area and/or its reduced efficiency (11,31). These changes may be attributed to a reduction in chlorophyll content (3,18,20) and/or abnormalities in the structure and function of chloroplasts (19,23). Conversely, transpiration has been reported to increase, decrease, or not change following infection in different pathosystems. Accelerated water loss from infected host tissue has been attributed to epidermal rupture caused by pathogens (8,28), increased tissue permeability (30), or inhibition of stomatal closure (29). Reduction in water loss may result from disease-induced stomatal closure, reduction of air space by hyphae, obstruction of conducting tissue and stomata (8,28), foliar defoliation, and/or early withering of transpiring foliage.

Incorporation of the impact of the pathogen in a physiological crop growth model requires that the effects of the pathogen on gas exchange processes be quantified (20,26). However, only a few authors have described the quantitative relationship between disease intensity and change in the rate of photosynthesis or of transpiration (5,12,20,25). If a change in the physiological process is associated with host-pathogen trophic relationships, then it may be possible to predict and more efficiently design experiments to measure the response of a host plant to a given disease. This study was undertaken in order to compare the effects of several foliar diseases on gas exchange processes of host plants and to determine the quantitative basis of these effects for modeling purposes.

MATERIALS AND METHODS

Effects of disease intensity on photosynthesis and transpiration rates were conducted under field conditions. Measurements were undertaken in twelve pathosystems, including five annual and

TABLE 1. Pathosystems examined for quantifying the effect of foliar disease on photosynthesis and transpiration

Host	Scientific name of the host	Scientific name of the pathogen	Disease
Wheat	*Triticum aestivum*	*Puccinia recondita*	Leaf rust
Wheat	*Triticum aestivum*	*Erysiphe graminis*	Powdery mildew
Wheat	*Triticum aestivum*	*Mycosphaerella graminicola*	Septoria tritici blotch
Corn	*Zea mays*	*Puccinia sorghi*	Corn rust
Cucumber[a]	*Cucumis sativus*	*Pseudoperonospora cubensis*	Downy mildew
Cotton[b]	*Gossypium barbadense*	*Alternaria alternata*	Alternaria leaf spot
Pepper	*Capsicum annum*	*Leveillula taurica*	Powdery mildew
Mango	*Magnifera indica*	*Pestalotia magnifera*	Pestalotia
Peach	*Prunus davidiana*	*Sphaerotheca pannosa*	Powdery mildew
Grape	*Vitis vinifera*	*Uncinula necator*	Powdery mildew

[a] A cucumber crop showing leaf symptoms induced by fungicide-controlled downy mildew was examined as well.

[b] A cotton crop showing leaf symptoms induced by magnesium chloride was examined as well.

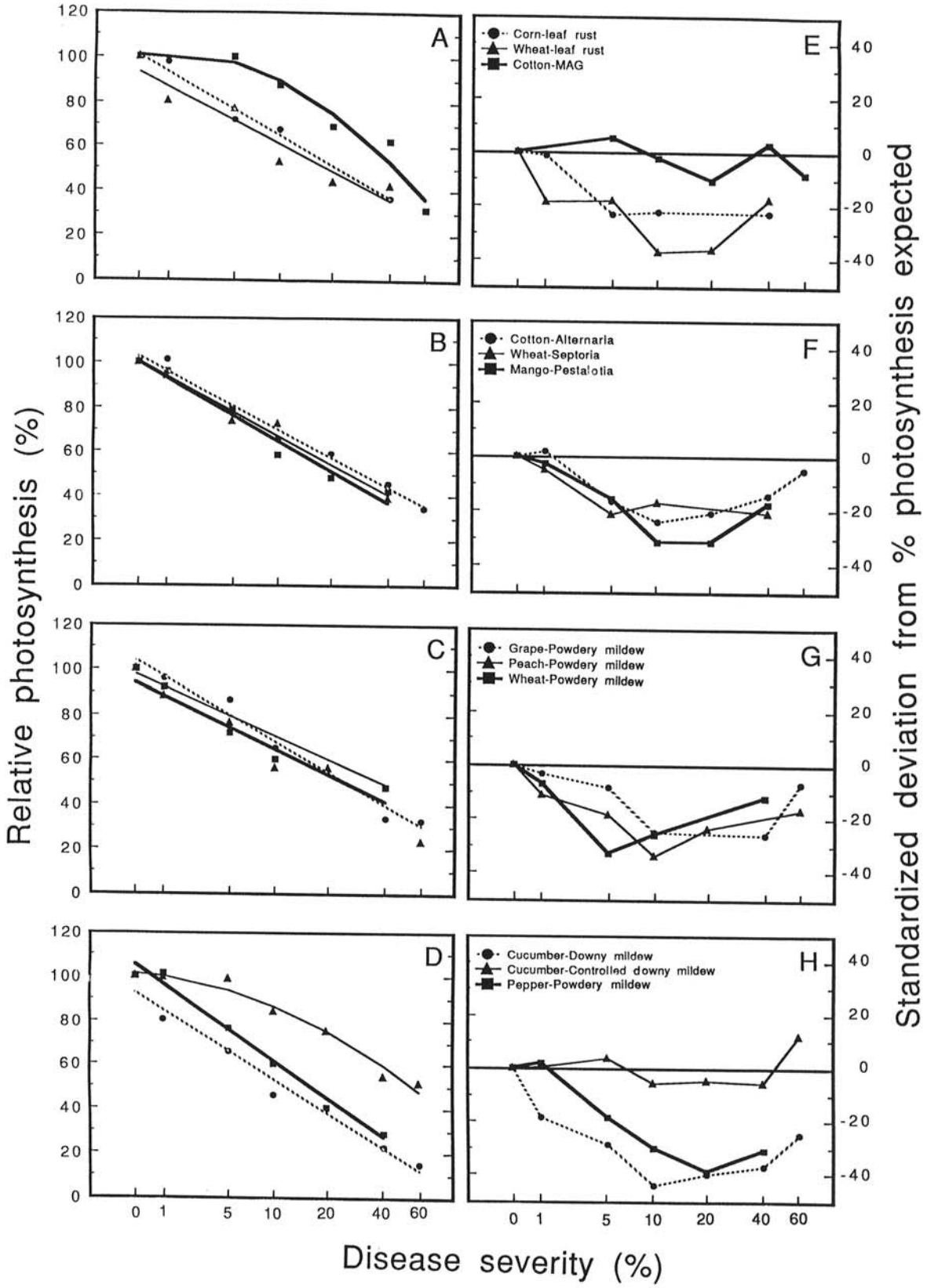

Fig. 1. A–D, Relationship between the relative photosynthesis rate and disease severity for several pathosystems. **E–H,** For each pathosystem the standardized deviation from percent photosynthesis expected was calculated as the difference between the expected and observed values. Calculation of the expected values was based on the assumption that the relative change in the process is equal to the proportion of the leaf area exhibiting disease symptoms. Regression parameter estimates for the relationships are presented in Table 2.

three perennial crops. Ten different foliar pathogens and two abiotic agents were studied (Table 1). Unless otherwise stated, disease intensities at the sites of measurement were not artificially manipulated (i.e., inoculation or fungicide spraying). Measurements were taken in commercial crops or in field trial plots located in the coastal plain or in the northern Negev regions of Israel. The field experiments were conducted for various epidemiological studies in addition to the present study. Methods of sowing, fertilizing, irrigation, and other cultural practices for each crop were as recommended to commercial growers in Israel. For each of the 12 pathosystems, measurements were taken on at least two different occasions. Because overall trends were similar, results of only one set of measurements are presented.

Diseases were monitored visually in the field using standard area diagrams. For some pathosystems, previously published diagrams (13) were used. For the rest, disease area diagrams were devised according to James (14), specifying seven levels of disease severity (i.e., proportion of leaf area exhibiting disease symptoms): 0, 1, 5, 10, 20, 40, and 60%. In all pathosystems it was possible to find leaves infected at most levels of disease severity.

A portable photosynthesis monitoring system (Model LI-6000, LI-COR, Inc., Lincoln, NE) was used to measure the rate of photosynthesis per unit leaf area (mg $CO_2/m^2/s$) and the rate of transpiration per unit leaf area (mg $H_2O/m^2/s$). Measurements were taken around noon (11:30 a.m.–1:30 p.m.), at a radiation intensity of 1200–1800 μmole/m^2/s photosynthetically active radiation, under clear sky conditions. Leaves to be assessed were selected at random on the basis of disease severity. In each of the pathosystems, five to 10 leaf replicates were selected for each of the seven levels of disease severity. While selecting leaves for measurements, an attempt was made to reduce variability not related to disease as much as possible (i.e., selected leaves were of approximately similar age, positioned in similar places on the host, etc.). The duration of each observation (i.e., the time during which the leaf was in the measurement chamber) was 42–60 s. During that time seven to 10 measurements of CO_2 concentration and relative humidity were recorded by the LI-COR system. The area of each of the sampled leaves was assessed in the field by comparison of the leaf with an illustrative scale depicting 10 leaf sizes. These scales had been prepared for each crop by means of a leaf area meter (Model LI-3000, LI-COR).

In addition to the diseases induced by fungi, some leaf symptoms caused by abiotic agents were studied. In these plants, leaves were selected and gas exchange rates measured as described above for the pathogenic agents. A cucumber crop infected by downy mildew had been subjected to intensive spraying of Maneb (Agan Ltd., Ashdod, Israel) applied weekly at a rate of 2.0 kg a.i./ha. The fungicide, together with the hot, dry weather conditions prevailing in the region before the time of measurement, had suppressed the pathogen. We considered the damage caused to the foliage (at the time of observation) as a reflection of stress imposed by an abiotic agent, because at that time the lesions were brown and necrotic. In addition, no signs of the fungus (i.e., sporangiophores or sporangia) were observed microscopically after infected leaves had been kept in a moist chamber for 48 h. Measurements were also taken in a cotton crop damaged by magnesium chloride (MAG), a chemical used for defoliation of cotton before harvesting. When applied at low concentrations, MAG causes circular brown necrotic lesions similar in size and shape to those induced by Alternaria leaf spot. Solutions containing 0, 1, 2, 4, 6, 8, 10, 14, or 18% MAG in 100 ml water were applied via a back-sprayer to cotton plots 4 × 2 m in area, thus producing a gradient in the severity of foliar damage.

A transformation, natural logarithm of disease severity plus e (2.718), was used to stabilize variance and linearize the relationship between gas exchange processes and disease severity (10). So that data from disease-free leaves could be included in the analyses, the constant e was added to proportional severity values. Adjustments for differences in the rate of photosynthesis and transpiration among the different pathosystems and sampling dates were achieved by expression of the gas exchange variables relative to the values obtained simultaneously for disease-free leaves.

Effects of each disease on gas exchange processes of the host crop were quantified by means of regression analysis. The dependent variable in all analyses was the relative rate of photosynthesis or transpiration, and the independent variable was the natural logarithm (plus e) of disease severity. First- and second-order polynomials were adjusted for each data set. The precision of each of the regression models was determined using several statistical parameters, including the coefficient of determination (R^2), the error variance, and the significance of the regression model as determined by the F test. One model was selected to fit each data set.

In some analyses, a standardized deviation from the expected values was calculated for the relative rates of photosynthesis or transpiration. Standardized deviations were calculated as the difference between the observed rate of each process and the expected rate. Estimation of the expected rates was based on the assumption that the relative change in the process is equal to the proportion of leaf area exhibiting disease symptoms. As an example, for 60% disease severity the expected rate of photosynthesis or transpiration was 40%. Standardized deviations (SD) were plotted against disease severity values (DS), and the relative area under the standardized deviation curve (RAUSDC) was calculated as:

$$\text{RAUSDC} = \left[\sum_{i=1}^{n} (SD_{i+1} + SD_i)(DS_{i+1} - DS_i) / 2 \right] / (DS_n - DS_1)$$

RAUSDC values were used to compare the effects of different diseases on the rates of photosynthesis or transpiration of their host crops.

TABLE 2. Regression parameter estimates expressing the relationship between the relative photosynthesis rate per unit of leaf area and natural logarithm (plus e) of disease severity for different pathosystems

Host	Disease	Regression model	R^2(%)[a]	F	P
Wheat	Leaf rust	114−20.9X	90.6	38.8	0.003
Wheat	Powdery mildew	113−19.1X	87.0	20.0	0.02
Wheat	Septoria tritici blotch	122−21.7X	97.7	126.3	0.002
Corn	Corn rust	124−23.3X	98.3	172.3	0.001
Cucumber	Downy mildew	118−25.6X	97.6	207.2	<0.001
Cucumber	Controlled downy mildew	$98.9+6.8X-4.6X^2$	97.1	67.9	0.001
Cotton	Alternaria leaf spot	124−21.3X	98.6	348.1	<0.001
Cotton	MAG[b]	$86.6+22.1X-8.3X^2$	95.5	31.9	0.01
Pepper	Powdery mildew	133−28.2X	98.4	253.9	<0.001
Mango	Pestalotia	123−22.9X	96.9	124.7	<0.001
Peach	Powdery mildew	121−23.1X	97.0	127.3	<0.001
Grape	Powdery mildew	127−23.3X	97.7	168.7	<0.001

[a] Coefficient of determination.
[b] Symptoms induced by magnesium chloride.

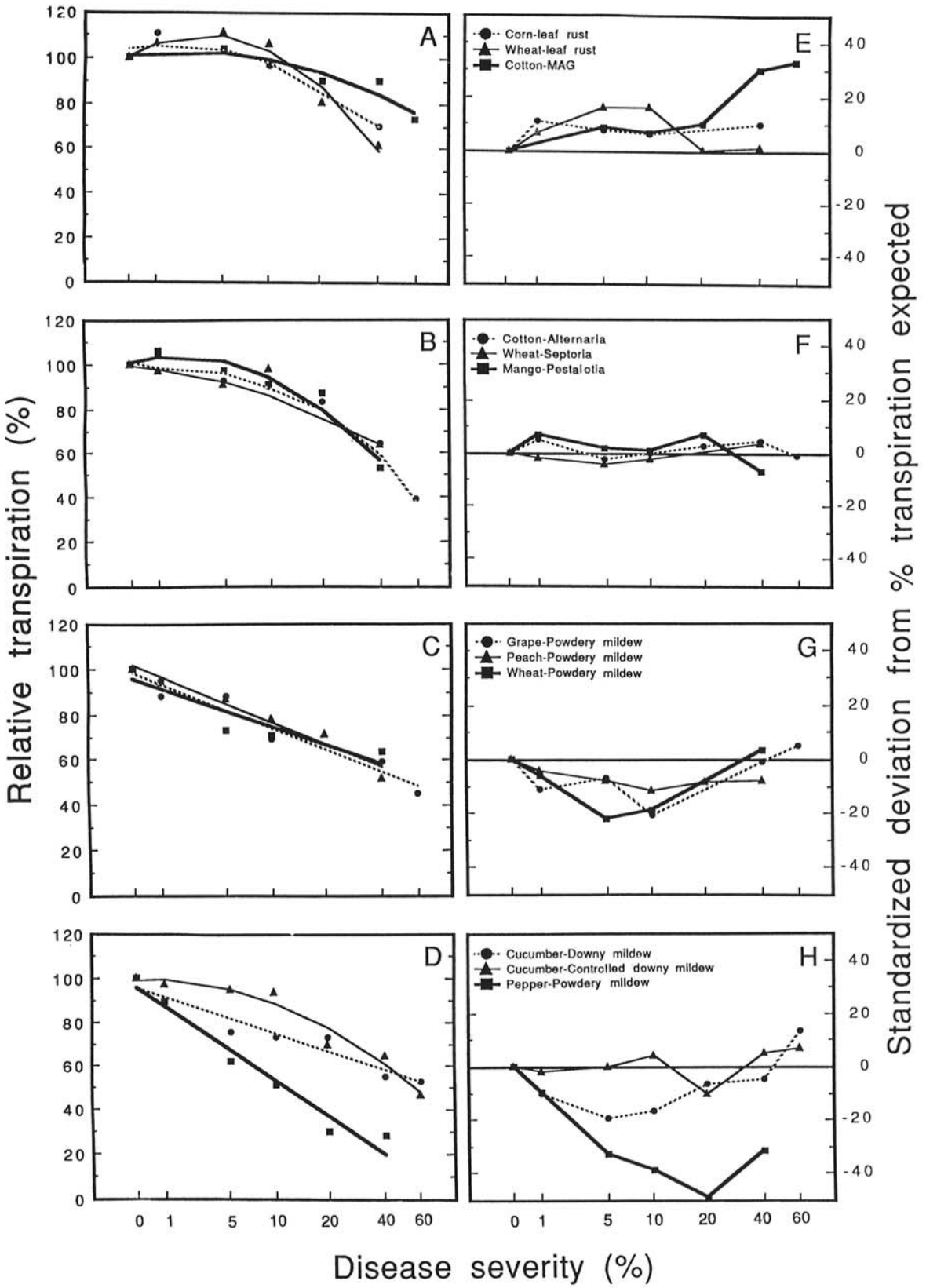

Fig. 2. A–D, Relationship between the relative transpiration rate and disease severity for several pathosystems. **E–H,** For each pathosystem the standardized deviation from percent transpiration expected was calculated as the difference between the expected and observed values. Calculation of the expected values was based on the assumption that the relative change in the process is equal to the proportion of the leaf area exhibiting disease symptoms. Regression parameter estimates for the relationships are presented in Table 3.

TABLE 3. Regression parameter estimates expressing the relationship between the relative transpiration rate per unit of leaf area and natural logarithm (plus e) of disease severity for different pathosystems

Host	Disease	Regression model	R^2(%)[a]	F	P
Wheat	Leaf rust	$63.9+50.6X-13.9X^2$	96.9	47.6	0.005
Wheat	Powdery mildew	$109-13.5X$	86.2	18.7	0.02
Wheat	Septoria tritici blotch	$98.3+4.4X-3.6X^2$	99.3	132.9	0.007
Corn	Corn rust	$89.0+21.8X-7.2X^2$	95.4	20.5	0.04
Cucumber	Downy mildew	109-13.5X	93.2	68.7	<0.001
Cucumber	Controlled downy mildew	$90.7+14.1X-5.9X^2$	95.7	44.1	0.002
Cotton	Alternaria leaf spot	$85.0+22.6X-7.9X^2$	96.5	55.6	0.001
Cotton	MAG[b]	$90.3+14.3X-4.3X^2$	88.5	11.5	0.03
Pepper	Powdery mildew	$123-27.6X$	95.9	92.7	<0.001
Mango	Pestalotia	$80.4+30.0X-9.7X^2$	94.2	24.3	0.01
Peach	Powdery mildew	$118-16.2X$	96.3	103.3	0.001
Grape	Powdery mildew	$114-15.8X$	94.2	65.2	0.001

[a]Coefficient of determination.
[b]Symptoms induced by magnesium chloride.

RESULTS

Regardless of the pathosystem, photosynthesis was affected in a similar manner—i.e., a linear decrease with increments of the natural logarithm of disease severity. In addition, the reduction was greater than would be expected on the bassis of the proportion of healthy leaf area reduction. Photosynthesis was reduced by the abiotic agents as well, but the amount of decrease was close to the expected values (Fig. 1 and Table 2).

In general, the relative rate of transpiration decreased with increments in disease severity for both the pathogenic and the abiotic agents. However, the amount of decrease varied substantially among the different pathosystems. At low levels of infection (severity < 10%), transpiration was increased in rust-infected leaves (in corn and wheat) compared to disease-free leaves. At higher rust severities and at all severities of MAG (in cotton) transpiration was reduced, but the reduction was smaller than expected from the proportion of leaf area affected. Alternaria leaf spot (in cotton), Septoria tritici blotch (in wheat), Pestalotia (in mango), and fungicide-controlled downy mildew (in cucumber) reduced transpiration, yielding rates close to values expected due to loss of green leaf area alone. Powdery mildews (in wheat, pepper, peach, and grape) and downy mildew (in cucumber) reduced transpiration more than would be expected on the basis of the proportional reduction in leaf area (Fig. 2 and Table 3).

A general representation for the effect of diseases on gas exchange processes was attained by plotting of RAUSDC from percent of transpiration expected against RAUSDC from percent of photosynthesis expected (Fig. 3). According to the differences in RAUSDC from the expected percentages, these effects were considered as marginal (0–0.05 units difference), slight (0.05–0.25 units difference), or substantial (>0.25 units difference). Several patterns of effects were thus identified for the different pathosystems: marginal effects on both processes (such as those induced by controlled downy mildew), marginal effect on photosynthesis and slight increase in transpiration (MAG), slight decrease in photosynthesis and slight increase in transpiration (rusts), slight decrease in photosynthesis and marginal effect on transpiration (Alternaria leaf spot, Septoria tritici blotch, and Pestalotia), slight decrease in photosynthesis and slight decrease in transpiration (powdery mildews in wheat, peach and grape), substantial decrease in photosynthesis and slight decrease in transpiration (downy mildew), and substantial decreases in both photosynthesis and transpiration (powdery mildew in pepper).

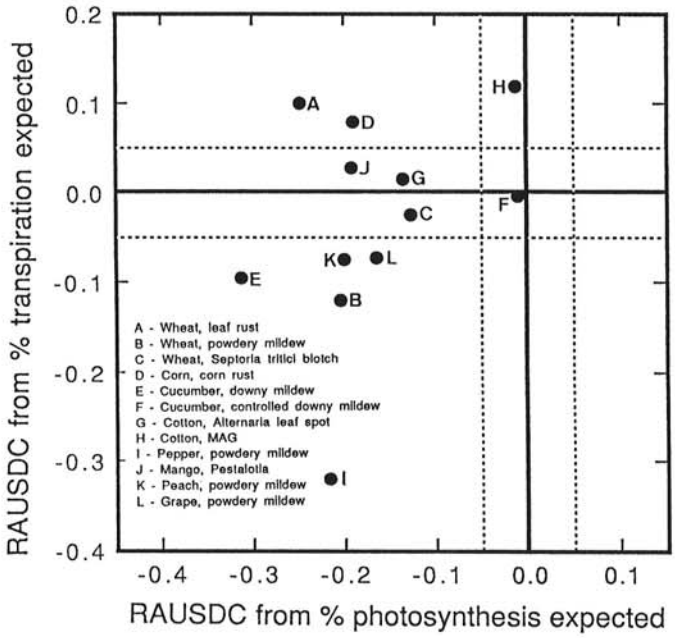

Fig. 3. Relationship between the relative area under the standardized deviation curve (RAUSDC) from percent transpiration expected and RAUSDC from percent photosynthesis expected, for 12 different pathosystems. Calculation of the expected values was based on the assumption that the relative change in the process is equal to the proportion of the leaf area exhibiting disease symptoms. The procedure for RAUSDC calculation is described in the text. Horizontal and vertical dotted lines indicate 5% difference in RAUSDC from zero. Letters indicate the identity of each pathosystem.

DISCUSSION

The photosynthetic and transpirational activities of the host plants were reduced by all diseases considered in this study. Theoretically (12,26), in relation to disease-free leaf area, the reduction in rate of the physiological processes may be a) proportional, b) proportionally greater, or c) proportionally smaller than the corresponding reduction of healthy leaf area due to disease.

In this study the proportional photosynthesis response was observed in crops affected by the abiotic agents. Proportional transpiration response was observed in crops infected by pathogens causing necrotic lesions (Alternaria leaf spot, Septoria tritici blotch, and Pestalotia) (Figs. 1 and 2). No particular physiological explanation appears necessary for the proportional response. Cells penetrated by fungal structures (haustoria or hyphae) or killed by secretion of enzymes lose their chlorophyll and presumably their capacity to photosynthesize or transpire. In this case the destruction of cells is directly related to the presence of the fungus, and uncolonized portions of the leaf remain normally active. The effect of infection on the physiological processes appears to be completely accounted for by the loss of leaf area to the pathogen.

The proportionally greater response is associated with pathogenic influence beyond the diseased area. Low levels of disease may have a disproportionately large effect on host metabolism. One possible explanation for this is that the fungus secretes enzymes or phytotoxic compounds that diffuse to uncolonized portions of the leaf, or, while acting as a strong

sink, the fungus absorbs carbohydrates and other nutrients from uncolonized portions of the leaf. Thus, the area affected by the pathogen is greater than the area it invades (1,2,6). Another explanation is that visual assessments of the diseased area do not adequately reflect the portion of the leaf actually invaded by the pathogen. It is possible that mycelia grow and affect host cells beyond the visually recognizable lesions. Proportionally greater photosynthesis response was observed for all pathosystems in this study (Fig. 1) and was reported by other authors as well (5,12,20,25). Proportionally greater transpiration response was observed in crops affected by mildews (Fig. 2).

Proportionally smaller photosynthesis response may be associated with pathogenic fungi that exhibit a delicate type of parasitism, as in the case of some obligate parasites. Chlorophyll in the invaded host cells may be affected yet not completely destroyed by fungal intrusion. Infected leaf tissue may remain at least partially active. Proportionally smaller photosynthesis response was not observed in our study but was demonstrated by other authors (7,21). Transpiration of corn and wheat infected by rust, as well as of cotton affected by MAG, exhibited the proportionally smaller response. In fact, at low levels of rust infection (severities $<10\%$) the transpiration rate exceeded that of disease-free leaves. At disease severities higher than 10%, the infected leaves transpired less than uninfected leaves, but the decline in transpiration was smaller than would be expected on the basis of the reduction in uninfected leaf area (Fig. 2). Intensification of transpiration rates caused by rust fungi has been attributed to epidermal rupture caused by the pathogen (8,28).

Our results support previous observations (25) that visual estimates of infection may not always give a good indication of the effect of pathogens on host physiology. Visual assessments of disease may provide adequate estimates of physiological damage in certain pathosystems (e.g., effects of abiotic agents on photosynthesis or of fungus-induced necrotic lesions on transpiration) but not in others.

By comparing host-parasite interactions in the different pathosystems, we were able to formulate certain generalizations concerning the effect of diseases on photosynthesis and transpiration. The pattern of the host response to infection was not always related to the systematic group of either the host or the pathogen. The pattern of the response and the actual reduction in photosynthesis and transpiration were, however, related to the type of trophic relationships. This conclusion is illustrated in Fig. 3. Rusts in corn and wheat increased transpiration relative to the expected effects (proportionally smaller response); fungi causing necrotic lesions in cotton, wheat, and mango reduced photosynthesis (proportionally greater response) but did not substantially affect transpiration (proportional response); powdery mildews in wheat, peach, and grape reduced both photosynthesis and transpiration (proportionally greater response) but produced a substantially different effect in pepper. However, some of the characteristics of *Leveillula taurica*, the causal agent of powdery mildew in pepper, differ fundamentally from those of most other powdery mildews; it is an endoparasite and its path of infection is through the stomata (24).

The results presented in this article provide appropriate data sets for coupling of the effects of foliar diseases to crop growth simulators. We have already used the data set for wheat and Septoria tritici blotch and incorporated the effects of Septoria into a spring wheat growth model. The model was then used to test hypotheses concerning the effects of Septoria tritici blotch on wheat yields under the semiarid conditions of Israel (27).

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