Net Photosynthesis, Growth, and Transpiration in American Elm Seedlings as Influenced by Dutch Elm Disease and Plant-Water Stress

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ABSTRACT

Young American elm seedlings were inoculated with the Dutch elm disease pathogen or subjected to plant-water stress prior to measuring net photosynthesis, growth, and transpiration for a period of 5 weeks. Both treatments resulted in depressed growth when compared to untreated controls. The data for net photosynthesis and transpiration suggest that the pattern of symptom development in inoculated seedlings is different from plants experiencing an internal moisture deficit.

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The symptomatology of Dutch elm disease (DED) in susceptible American elms (*Ulmus americana* L.) resembles that of seedlings subjected to plant-water stress. The similarity of these two disorders has resulted in speculation that the wilting syndrome in DED results from a mechanical blockage of the water conducting system within infected plants (1, 6, 11). In the physiology of parasitism, relatively few studies have been made on the photosynthesis of diseased plants. This is particularly true with regard to the vascular wilt diseases, and little or no information is available regarding CO_2 uptake in elm seedlings infected with *Ceratocystis ulmi* (Buism.) C. Moreau. The purpose of this investigation was to observe the effect of DED on apparent or net photosynthesis, growth, and water loss in susceptible American elms, and to relate these findings to similar observations made on comparable *U. americana* seedlings subjected to plant-moisture stress.

MATERIALS AND METHODS.—A total of 50 21-month-old American elm seedlings were brought into the greenhouse in April and potted in 7-inch plastic containers using a 2:1:1 mix of soil-peat-perlite. After 3 weeks, all plants had broken dormancy, and abundant new foliage was evident. On 1 May, 30 seedlings were removed from the potting medium, the roots washed and blotted dry, and fresh weight values for each plant recorded. After replanting in the same plastic containers (this time lined with a polyethylene bag), the seedlings were placed in a humid greenhouse for 2 weeks prior to starting the study. On 1 May, 5 additional plants were selected and, after the fresh weight was determined as described above, they were oven-dried at 90 C for 48 hr, and subsequent dry weight values obtained. The relationship between fresh weight and dry weight for these 5 plants was used to estimate the initial dry weight of the 30 seedlings previously mentioned. The remaining 15 seedlings were grown with the others, and harvested at periodic intervals to determine leaf surface area.

Two weeks after transplanting, all seedlings were watered thoroughly, weighed, and transferred to a growth chamber maintained at a constant thermoperiod (24 C day, 18.5 C night) and photoperiod (2,200 ft-c combined incandescent, cool-white fluorescent light from 8 AM to 6 PM). At this time, the polyethylene liner in each container was securely fastened around the stem to prevent the evaporation of water vapor from the soil surface. Subsequent transpiration measurements were made gravimetrically (8).

On a Monday in mid-May, 6 plants were individually weighed, rewatered to their original weight with a dilute commercial fertilizer solution, and transferred to a closed system for measurement of CO_2 uptake by infrared gas analysis (Fig. 1). Carbon dioxide exchange was measured for a minimum of 0.5 hr. Light intensity in the photosynthesis chamber was similar to that in the growth chamber, thus eliminating the necessity for extended periods of adjustment. Temperature and relative humidity in the chamber were 25 ± 1.5 C and 43 ± 5%, respectively. After the initial photosynthetic rate of each seedling was obtained, treatment was initiated and the plants were returned to the growth chamber. Treatment consisted of either (i) inoculation with a conidial suspension of *C. ulmi* (3 ml; 2.01 × 10^6 conidia/ml) prepared from isolates representing several different geographical areas and

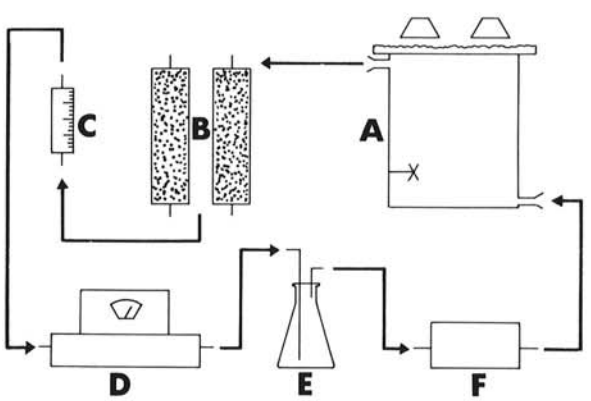

Fig. 1. Diagrammatic representation of closed system for measuring net photosynthesis in American elm seedlings. A = photosynthesis chamber; B = silica gel water vapor traps; C = flow meter; D = infrared gas analyzer; E = air reservoir; F = pump.

inoculated with the technique of Gregory (3); (ii) withholding water to induce an internal plant-moisture deficiency; or (iii) untreated control.

Measurements of photosynthesis and transpiration were recorded daily for 6 additional seedlings on Tuesday through Friday. The moisture lost during transpiration was replaced daily in treatments i and iii by opening the polyethylene liner and adding water while the seedling was still on the balance. This measuring sequence was repeated weekly for 5 weeks. Each Wednesday during the study, 3 seedlings from the group of 15 plants mentioned earlier were harvested, and their respective leaf surface areas determined by planimetry. These determinations were used in computing the CO_2 uptake and water vapor loss per unit leaf surface area for all seedlings during that particular week. Upon termination of the experiment, all 30 seedlings were harvested for fresh and dry weight determinations. In addition, inoculated seedlings were observed for foliar symptoms, xylem discoloration, and basal stem sprout formation, all characteristic symptoms of DED. Isolations were also made from stem sections of each inoculated seedling to determine if *C. ulmi* was present.

RESULTS.—There were significant increases in both fresh and dry weights for all treatments (Table 1). As anticipated, the growth of both inoculated and moisture-stressed seedlings was considerably less than the untreated controls. In the case of dry weight, which is probably a better indicator of over-all growth, both the stress treatments grew only half as much as the controls. Although both stress treatments showed comparable changes in dry weight after the 5-week period, the pattern of growth for these two treatments was different. In the early stages of treatment, the water-stressed elms showed considerably more growth than comparable inoculated seedlings. However, in the latter stages of the study, the reverse situation occurred. This was apparently caused by the rather profuse formation of basal stem sprouts which developed on DED seedlings during the last week or 2 of the study. These sprouts, which are characteristic of DED (7), are also responsible for the considerable difference in fresh weight observed between inoculated and water-stressed plants in Table 1, since they constitute young, succulent tissue.

The differences in growth pattern of the two stress treatments are also reflected in the measurements of apparent photosynthesis (Table 2). After the first 2 weeks, the photosynthetic rate of water deficient elm seedlings is only 4% less than the untreated controls. During the same period, apparent photosynthesis of DED seedlings declined 33%. By the end of 5 weeks, however, CO_2 uptake had decreased 86% in plants from which water had been withheld, and only 41% from inoculated seedlings. The dissimilarity in photosynthetic response of the two stress treatments in this study suggests that the mechanism responsible for development of symptoms differs in inoculated as opposed to moisture-deficient elms. This suggestion is supported by the transpiration data found in Table 3. These data indicate that water loss and apparent photosynthesis follow a very similar pattern in water-stressed elm seedlings. This similarity is expected, as both photosynthesis and transpiration rely primarily on stomata to provide a pathway for the exchange of CO_2 and water vapor. This same relationship has some disparities in the case of DED seedlings, however. As the uptake of CO_2 declines significantly (47%) between the 1st and 2nd week of the experiment, transpiration decreases only 10%. Thus, despite a relatively free pathway for CO_2 exchange, photosynthesis is suppressed drastically.

DISCUSSION.—The data from this study show that both internal moisture deficiency and DED development are effective in reducing the growth of American elm. The mechanism by which growth is suppressed seems somewhat different for the two treatments. Photosynthesis is actually inhibited in DED seedlings even when transpiration is quite active. This suggests that some metabolic disturbance is

TABLE 1. Growth response of 21-month-old American elm seedlings as influenced by moisture stress and Dutch elm disease for a period of 5 weeks[a]

Treatment	Fresh weight		Dry weight	
	Initial (g)	Final (g)	Initial[b] (g)	Final (g)
Inoculated	24.0	39.6	12.3	16.3
Water-stressed	22.8	33.9	11.7	15.5
Control	22.3	56.2	11.4	19.0

[a]Values are the mean of 10 determinations.
[b]Estimated.

TABLE 2. Photosynthetic response of 21-month-old American elm seedlings as influenced by moisture stress and Dutch elm disease

Treatment	Photosynthesis (mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$)[a]				
	1st wk	2nd wk	3rd wk	4th wk	5th wk
Inoculated	1.40	0.74	0.56	0.45	0.49
Water-stressed	1.42	1.07	0.62	0.26	0.12
Control	1.57	1.11	1.05	0.80	0.83

[a]Values are the mean of 10 determinations expressed in milligrams of carbon dioxide absorbed per square decimeter of leaf surface area per hour.

TABLE 3. Loss of water vapor from 21-month-old American elm seedlings as influenced by plant-water stress and Dutch elm disease

Treatment	Transpiration ($g \cdot dm^{-2} \cdot wk^{-1}$)[a]				
	1st wk	2nd wk	3rd wk	4th wk	5th wk
Inoculated	1.39	1.25	0.60	0.39	0.52
Water-stressed	1.41	1.25	0.84	0.35	0.21
Control	1.41	1.26	1.30	1.11	1.32

[a]Values are the mean of 10 determinations expressed in grams of water lost per square decimeter of leaf surface area per week.

responsible for depressed photosynthesis, thus giving credence to proponents of the toxin (2, 4, 9, 12) or nutritional (10) theories of disease development. Additional metabolic studies should be conducted on inoculated and moisture-stressed elms to assess the importance of this relationship.

The photosynthetic rates reported in this investigation are somewhat less than those reported for other deciduous woody plants. The maximum CO_2 uptake observed in untreated (control) elm seedlings was 1.7 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$, whereas Kramer (5) reports values considerably greater than this for various species of birch, beech, dogwood, and oak.

Development of symptoms in DED is often erratic. To determine successful infection of the host, each inoculated seedling was observed for foliar symptoms, xylem discoloration, and basal stem sprout formation. In addition, isolations from individual stem sections were made on acidified potato-dextrose agar to test for the presence of *C. ulmi*. The stems from all inoculated plants showed vascular discoloration, but it was not possible to isolate the causal organism in every instance. Sixty per cent of the inoculated seedlings exhibited foliar wilt, and 80% had basal stem sprouts by the end of 5 weeks. Although every seedling tested positive for two or more DED symptoms, it is doubtful that all plants were colonized equally by the fungus. This disparity confounds the assessment of physiological response to DED infection.

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