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Effects of Soil Flooding on Leaf Gas Exchange of Seedling Pecan Trees

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Abstract. **Roots of 53-day-old pecan seedlings [*Carya illinoensis* (Wangenh.) C. Koch] were either not flooded or flooded by submerging pots to ≈2 cm above the soil line in containers of water. Leaf gas exchange measurements at 1000 $\mu mol \cdot s^{-1} \cdot m^{-2}$ photosynthetic photon flux, 340 $\mu l \cdot liter^{-1}$ CO_2, and 27°C were made prior to flooding, after 1, 8, or 15 days of flooding, and 7, 14, or 21 days after flooding was terminated. Net CO_2 assimilation rate (A) decreased 56% after 1 day of flooding. Flooding 9 or 15 days did not further depress A. Carbon assimilation of trees that had been flooded for 8 days and then returned to nonflooded soil for 7 days were similar to unflooded trees. In contrast, A of seedlings flooded 15 days did not regain the A of unflooded trees 14 days after flooding terminated. Transpiration rates (E) paralleled A in all treatments. Leaf conductance to CO_2 (g_L) was positively correlated with A ($R^2 = 0.94$). However, leaf internal CO^2 (C_i) concentration was not decreased by reduced g_L. Water potential (ψ_L) and turgor potential (ψ_p) of leaves were higher when trees were flooded, but osmotic potential (ψ_s) was unaffected.**

Soil flooding has been observed to reduce A in pecan (14), as well as other herbaceous and woody species (4–6, 15, 17–20, 26). Leaf stomatal closure normally accompanies soil flooding (1, 2, 4, 6, 8, 9, 12, 15, 16, 18, 19, 21, 23). In some species, stomatal closure due to soil flooding results from low ψ_L (more negative) (13, 24), but, in other species, stomatal closure prevents a decline in ψ_L (3, 12, 16, 23, 25). Root flooding may reduce both leaf mesophyll and stomatal conductance (6, 7, 15, 19), thus reducing A. Photorespiration may be increased by soil flooding; however, Bradford (4) reported that photorespiration of tomato was not increased by short-term flooding, although A was decreased.

Our three objectives were: 1) to determine the effect of soil flooding on A, g_L, E, and C_i of pecan leaves; 2) to determine if stomatal closure, frequently associated with flooding, was due to low ψ_L or some other mechanism; and 3) to determine the effect of flooding duration on leaf gas exchange and the extent to which trees recover after exposure to soil flooding.

Stratified seeds of 'Dodd' were bathed in an aerated 100-ppm GA_3 solution for 1 week, then transferred to aerated water until radicle emergence. Seeds with uniform radicle length were planted 12 June 1986 in 25-cm-diameter × 23-cm-high containers filled with a fire-hardened calcite clay (Turface, Wyandotte Chem. Corp., Wyandotte, Mich.). The growing medium was amended (in $g \cdot m^{-3}$) with 3530 18N–2.6P–10K (Osmocote slow-release fertilizer, Sierra Chemical Co., Milpitas, Calif.), 4694 dolomite, 882 0N–20P–0K, 480 $FeSO_4$ (25% Fe), 92 $MnSO_4$ (27% Mn), 21 $CuSO_4$ (25.4% Cu), 3.5 $NaBO_2$ (20.5% B), 0.5 $NaMoO_4$ (39% Mo), and 39 $ZnSO_4$ (36% Zn). Plants were grown in a greenhouse with temperature controls set for 21°C night and 27° day, but day temperatures frequently reached 38°. A weekly spray schedule alternating *O,S*-dimethyl acetylphosphoramidothioate (acephate) and (RS)-α-cyano-3-phenoxybenzyl 2,2,3,3-tetramethylcyclopropanecarboxylate (fenpropathrin) at recommended rates was used to prevent insect infestation. Trees were watered as required.

Excess trees were grown to allow selection of uniform 53-day-old trees for each block. Preflooding measurements were made as described below, then tree roots were either not flooded (control) or flooded. Roots were flooded by submerging the pots in individual containers of water to ≈2 cm above the soil line. Gas exchange measurements were made prior to flooding, after trees had been flooded 1, 8, or 15 days, and when trees were returned to nonflooded soil (normal watering) for 7, 14, or 21 days after 8 or 15 days of flooding. Each treatment contained five single-tree replications in a randomized complete block design. Trees were blocked by visual appearance, and flooding dates were staggered in such a manner to allow gas exchange measurements on one block each day. Data were analyzed using the *t* test and A and g_L were correlated using linear regression.

Gas exchange parameters were measured in a flow-through system using a 14 × 14.5 × 20 cm plexiglass chamber with a water-jacketed aluminum base. Chamber temperature was controlled at 27 ± 0.5°C by circulating water from a refrigerated water bath through the aluminum base. The chamber was equipped with a circulating fan to minimize boundary layer resistance. The air source was compressed industrial air (≈340 $\mu l \cdot liter^{-1}$ CO_2, 21% O_2), regulated with flow controllers, and humidified to about 70% RH by passing the air stream over water in an ice bath. Carbon dioxide and water vapor exchange were measured with a differential Horiba PIR 2000 infrared gas analyzer (Irvine, Calif.) and EG & G model 911 dew point hygrometer (Waltham, Mass.), respectively. The air stream was passed through an ice bath trap to remove excess water prior to CO_2 measurement. Light was supplied from a 400-W General Electric metal halide lamp, which delivered 1000 $\mu mol \cdot s^{-1} \cdot m^{-2}$ photosynthetic photon flux (PPF) at the leaf surface. Gas exchange parameters were calculated as previously described (9, 10).

Two hours prior to measurements, trees

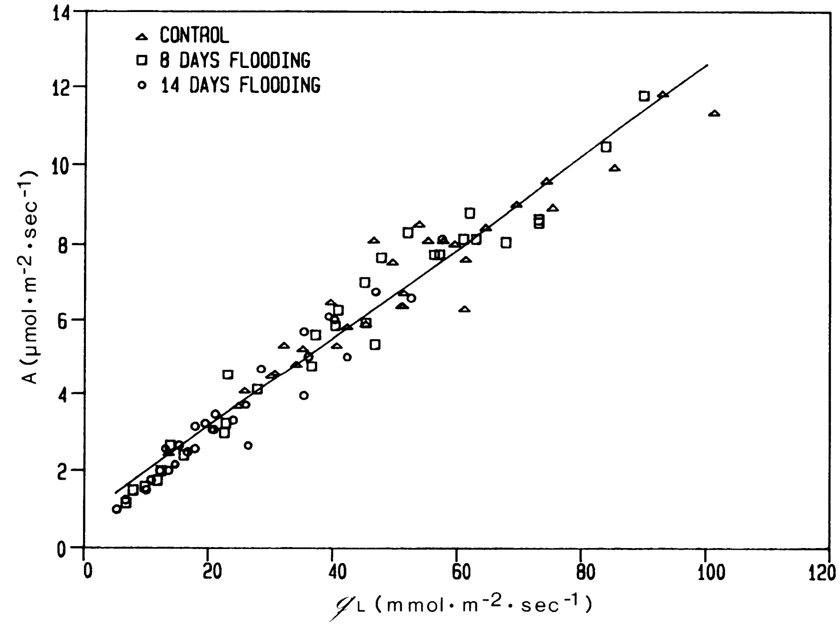

Fig. 1. The relationship of carbon assimilation (A) and leaf conductance to CO_2 (g_L) (R^2 = 0.94).

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Table 1. Flooding and postflooding effects on net CO_2 assimilation (A), transpiration (E), leaf water potential (ψ_L), leaf conductance to CO_2 (g_L), and leaf internal CO_2 concentration (C_i) of 'Dodd' pecan seedlings.

	Days flooded				Days drained				
					7		14		21
					Days flooded before draining		Days flooded before draining		Days flooded before draining
Treatment	0	1	8	15	8	15	8	15	8
					A (μmol·s^{-1}·m^{-2})				
Control	6.98	5.94	6.81	7.78	7.78	6.76	6.76	7.70	7.70
Flooded	6.21	2.56*	2.21*	2.61*	6.80	3.62*	6.95	5.67*	9.51
					E (mmol·s^{-1}·m^{-2})				
Control	1.71	1.50	1.86	2.07	2.07	1.89	1.89	2.38	2.38
Flooded	1.66	0.76*	0.61*	0.70*	1.73	0.94*	1.87	1.55*	2.92
					ψ_L (MPa)				
Control	−1.78	−1.70	−1.71	−1.68	−1.68	−1.94	−1.94	−1.48	−1.48
Flooded	−1.63	−1.47	−1.47*	−1.31*	−1.64	−1.63*	−1.79	−1.46	−1.53
					g_L (mmol·s^{-1}·m^{-2})				
Control	44.9	41.4	51.8	63.8	63.8	50.4	50.4	58.5	58.5
Flooded	45.3	16.7*	14.9*	18.7*	51.7	22.9*	47.6	37.5	74.0
					C_i (μl · liter^{-1})				
Control	167	169	172	178	178	161	161	171	17
Flooded	176	169	161	164	171	150	161	174	17

*Significantly different from the control at the 5% level.

were watered to minimize water stress. Measurements were made by placing the terminal leaflet from a recently matured leaf in the plexiglass chamber. Steady rates of A and E were obtained in 0.5 to 2 hr. Leaf and chamber temperatures were monitored with copper–constantan thermocouples. Gas exchange was measured on the same leaf of each plant throughout the experiment. Leaf area was determined by tracing the leaf after each measurement, and area was measured using a LI-COR model LI-3100 area meter. Area of the measurement leaf was confirmed upon termination of the experiment.

Water potential was measured using leaf cutter psychrometers (J.R.D. Merrill, Logan, Utah). Three 0.24-cm^2 disks were cut from one leaflet near the leaf used for gas exchange measurements and sealed in the psychrometers within 3 sec. Previous work has shown no significant differences in ψ_L among leaflets or leaves on seedlings of this size (unpublished data). Psychrometers were placed in a 30°C water bath for 2 hr, then wet bulb depression was read in microvolt output. The samples were read using a Wescor HP-115 water potential data system (Logan, Utah) set a 5 mA cooling current, 15 sec cooling time, and 5-sec delay. The microvolt readings were used with calibration equations derived for each psychrometer to calculate water potential values. Osmotic potential (ψ_s) was determined by killing the tissue in a freezer, then following the procedures outlined above. Turgor potential (ψ_p) was calculated as the difference in ψ_L and ψ_s.

One day of root flooding reduced A 56% and E 50%, compared to unflooded trees (Table 1). Net CO_2 assimilation and E after 8 and 15 days of flooding were similar to those after 1 day of flooding. Trees flooded for 8 days, then drained for 7 days, had A and E rates similar to unflooded trees. Although trees flooded for 15 days did not regain A and E of the unflooded trees 14 days after draining, A was enhanced substantially over flooded rates. Loustalot (14) reported a similar reduction in A of seedling pecans when flooded; however, A was not decreased until trees had been flooded 4 days. Flooding 35 days had reduced A about 50%, then containers were drained, and preflooding A levels occurred after 13 days. Sweet gum responded more rapidly than seedling pecans to flooding (18), as did the trees in this study. Assimilation, g_L, and E were sharply reduced within 24 hr of flooding.

Leaf ψ_L was higher in flooded trees than unflooded trees 8 days after flooding (Table 1). The higher ψ_L of flooded trees was associated with a change in leaf ψ_p, but not ψ_s after 1 day (unflooded trees: ψ_p = 0.69 MPa, ψ_s = −2.40 MPa; flooded trees ψ_p = 0.94 MPa, ψ_s = −2.45 MPa), and 7 days of flooding (unflooded trees: ψ_p = 0.67 MPa, ψ_s = −2.44 MPa; flooded trees ψ_p = 0.82 MPa, ψ_s = −2.35 MPa).

Leaf conductance to CO_2 was reduced by flooding (Table 1), and A and g_L were positively correlated ($R^2 = 0.94$) (Fig. 1). This correlation suggests the possibility that partial stomatal closure due to flooding was limiting A. However, C_i was not significantly different between flooded and unflooded trees (Table 1). Since C_i was not decreased, the primary limitation to A during flooding was a reduced capacity of the mesophyll to assimilate CO_2, and not a reduction in stomatal aperture. Davies and Flore (6, 7) reported that A, g_L and g_r (residual conductance) declined in blueberries when flooded. They attributed the initial decline in A to g_L, since C_i was lower in flooded plants, followed by a reduction in A due to both g_L and g_r. Guy and Wample (11) found that A was decreased, independent of g_L in sunflower. These results support out findings that A is reduced primarily by a reduction in the capacity of the mesophyll to assimilate CO_2. Stomatal regulation of CO_2 exchange may contribute to the reduction in A. Alternatively, our data suggest that the decreased A may directly or indirectly regulate stomatal opening. Decreased A increases the 3-phosphoglycerate pool size in the chloroplast at the expense of orthophosphate (22). Thus, chloroplast pH is decreased, which could release abscisic acid and induce partial stomatal closure. This process would account for the close correlation between A and g_L and the lack of response of C_i.

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Path Analysis of Chrysanthemum Growth and Development

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Abstract. **Plants of chrysanthemum (*Dendranthema grandiflora* Tzvelev.) were grown under one of 25 irradiance and temperature combinations from start of short days to flower. Four phases of development were defined as 1) the start of short days to the appearance of 4-mm terminal flower buds (phase I), 2) appearance of 4-mm terminal flower buds to removal of lateral flower buds when the terminal flower bud was 7 to 8 mm (phase II), 3) removal of lateral flower buds to flower buds showing first color (phase III), and 4) flower buds showing color to flowering (phase IV). Path analysis was used to study the influence of development time and relative dry weight gain during each of these four phases on development time and relative dry weight gain of subsequent phases. Relative dry matter accumulation during phases I, II, III, and IV significantly influenced cumulative relative dry weight gain, with phase I having the greatest influence. Increasing relative dry weight gain during phase I had a significant negative effect on relative dry weight gain in phase II. Time within each phase significantly affected total time to flower. Under the constant environmental conditions of this experiment, time in one phase did not influence the length of time in later phases.**

Recommendations have been developed to help growers produce high-quality flowering pot plants at low cost in minimal time. These recommendations often define a set of environmental conditions that are maintained during development through flowering (19, 20); however, constant environmental conditions throughout plant development may not optimize plant growth. If the plants respond differently to the environment during different phases of development, it should be possible to distinguish which phases of development are most important in determining total time of development and final plant characteristics. When these phasic responses have been quantified, it may be possible to more precisely monitor and control the environment during critical phases, while tolerating less control during other phases.

Wright (29, 30) developed a statistical method termed "path analysis" to quantify interactions among yield components and measure their contribution to total yield. In path analysis, the direct effects of independent variables are studied with the indirect effects removed. The advantage of such an analysis is that the effect of one component on another can be isolated from influences of other components. A high path coefficient between two components indicates that a change in one will result in a substantial relative change in the other when additional influences are removed. Path coefficients not significantly different from zero indicate that a change in one component will have little direct effect on a corresponding component. Path coefficients can be calculated only if their dependence structure is known. Yield components, for example, often develop sequentially, and those that develop late cannot affect early components. The directionality of dependencies can be determined in these situations.

Path analysis has been used by agronomists (8, 9) and horticulturists (11, 23, 25, 26) in problems involving yield. Analogies can be made between individual yield components and growth during discrete intervals, and between yield and final plant size. Yield components interact multiplicatively to produce yield, and a log transformation is used to make the dependence structure linear (24, 27). A log transformation also is used in the analysis of plant growth so that dry-matter accumulation can be expressed linearly when the percentage dry-weight increase is constant (16). This transformation also serves to equalize residual variance among young and mature plants, and removes any potential bias in favor of later growth phases. Both yield components and growth phases develop sequentially and the dependence structure can easily be determined.

Although several workers have described the growth of chrysanthemums by mathematical models (1, 7, 12, 14, 15, 18), none

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