

Sugarcane Photosynthesis, Transpiration, and Stomatal Conductance Due to Flooding and Water Table

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ABSTRACT

Sugarcane (*Saccharum* spp.) is the primary crop on the Histosols of the Everglades Agricultural Area (EAA), where periodic floods and undesirably high water tables are increasing in occurrence and duration. Improved understanding of the physiologic responses of sugarcane to these conditions could help develop strategies to sustain high yields. The purpose of this study was to evaluate the effects of periodic flooding followed by drainage to different depths on single-leaf net photosynthetic rate (Ps), transpiration (Ts), and stomatal conductance (SC) of sugarcane. In 2000 and 2001, two sugarcane genotypes were planted as split plots in 12 lysimeters filled with Pahokee muck soil. Responses of Ps, Ts, and SC to four water-table treatments were measured for four 21-d cycles each year. Three treatments consisted of 7-d flooding followed by 14-d drainage to depths of 16, 33, or 50 cm. The fourth treatment was a continuous 50-cm water table. Analyses of individual cycles and analyses repeated over cycles generally identified neutral or positive responses of Ps, Ts, or SC to flood. Drained water-table depth did not consistently affect Ps, Ts, or SC, but when differences occurred, 16 cm was often a favorable drainage depth. These neutral and sometimes positive responses to short-duration flood or long-duration high water tables support previous reports of acceptable and sometimes enhanced yields from sugarcane exposed to high water tables. Previous findings were supported that time of formation of stalk aerenchyma in sugarcane may be a key factor for sustaining high yields after exposure to flood.

THE EAA is a 280 000-ha basin of Histosols that lie on limestone bedrock in the northern region of the historic Everglades in Florida. Sugarcane is grown on about 148 000 ha in the EAA (Glaz, 2002). Before construction of an extensive public-private system of canals through the northern Everglades, the EAA was flooded most of the time (Snyder and Davidson, 1994). The canal system now facilitates the maintenance of desired water-table depths of 40 to 95 cm in sugarcane fields (Omary and Izuno, 1995).

Several factors have gradually resulted in sugarcane being periodically exposed to higher than desired water tables and floods in the EAA. Soil subsidence caused loss of depth in EAA Histosols at the rate of about 2.5 cm yr⁻¹ before 1978 (Shih et al., 1978). From 1978 until the most recent survey in 1997, the rate of soil loss declined to 1.4 cm yr⁻¹ (Shih et al., 1998). Some EAA fields had as much as 300 cm of soil above the limestone bedrock when they were first drained and used for agriculture. Depth of soil to bedrock varies, but a substantial

number of fields now have less than 40 cm of soil (Shih et al., 1998). Second, for every cm of rainfall, the free water in the soil profile of EAA Histosols can be expected to rise about 10 cm (Glaz et al., 2002). Finally, there are regulated and voluntary limits on pumping from farm ditches to public canals as a means of reducing P discharge to the natural Everglades.

The issues of soil subsidence and P discharge to the Everglades also provide incentives to maintain higher water tables and short-duration floods. The primary cause of subsidence in the EAA is microbial oxidation (Tate, 1980). The factor that most influences the rate of microbial oxidation is depth of water table in the soil profile. Therefore, the rates of oxidation and subsidence are directly proportional to the depth of the water table. If the distance between the water table and the soil surface is halved, the rate of subsidence is halved (Snyder et al., 1978).

Best management practices to reduce P discharge from the EAA often include strategies to reduce quantities and rates of pumping excess water from agricultural fields (Rice et al., 2002). After EAA sugarcane fields are flooded, which may occur several times during the summer rainy season, P export to the Everglades could be substantially reduced by allowing floods to subside more by evapotranspiration and less by pumping. Developing strategies that result in no yield loss to sugarcane after short-duration floods and increasing the duration of flood to which sugarcane is tolerant could facilitate farmers' efforts to conserve soil and reduce P discharge.

Previous research indicates that sugarcane maintains optimum yields through a wide range of water tables. Carter and Floyd (1971) reported that maintaining four constant water tables between depths of 61 and 122 cm during the active growth phase of sugarcane did not affect cane or sugar yields in Louisiana. Carter and Floyd (1975) maintained water tables at 30, 76, and 122 cm throughout the year in the second and third-ratoon crops of the plantings reported in their 1971 study. There were no significant differences in sugar yield in the second-ratoon crop, but in the third-ratoon crop, sugar yields decreased as water-table depth rose.

In a field study conducted in Florida, Kang et al. (1986) compared sugar concentration and cane yields of 16 clones of sugarcane (*Saccharum* spp.), one of *S. rosbustum* Brandes & Jesw. ex Grassl, one of *S. officinarum* L., and one of *Ripidium* spp. at water-table depths of 30 and 56 cm. Overall mean sugar concentration yields were 15.7 and 17.6% higher in the 30-cm water-table depth in the plant-cane and first-ratoon

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Abbreviations: CER, CO₂ exchange rates; EAA, Everglades Agricultural Area; Ps, single-leaf net photosynthetic rate; SC, single-leaf stomatal conductance rate; Ts, single-leaf transpiration rate.

crops, respectively. Overall mean cane yields were 27.5 and 25.3% higher in the 30-cm water-table depth in the plant-cane and first-ratoon crops, respectively. Gascho and Shih (1979) maintained water-table depths in lysimeters at 32, 61, and 84 cm. They reported that yields were optimum at 61 cm, but two of six cultivars had similar yields at all three water tables. Glaz et al. (2002) maintained, in the field, summer water-table depths of <15 cm and between 15 and 38 cm for plant-cane and first-ratoon sugarcane crops. Sugar yields at the water-table depth maintained at <15 cm were 92% of those at the deeper water table, and yield of one cultivar was reduced by 25% by the water-table depth of <15 cm. However, yields of two of nine cultivars were not affected by water table.

Mafizur Rahman et al. (1986) reported that flooding for one month reduced stalk growth rates by 40 to 88% in pots; variations were due to genotype. In Barbados, Webster and Eavis (1972) flooded sugarcane in lysimeters for 1, 4, 14, or 30 d at 1- and 3-mo age. During the floods, tiller formation and shoot growth were decreased, but increased growth after drainage relative to the nonflooded lysimeters resulted in similar yields for all treatments at 5-mo age. Although root weight was similar for all treatments at 5 mo, the sugarcane not exposed to flooding had fewer and larger roots than the flooded sugarcane. In a study conducted outdoors in large pots, Ray and Sinclair (personal communication, 2003) found that continuous flooding reduced sugarcane yields. However, they also found that a continuous water-table depth of 15 cm resulted in neutral or beneficial yield responses for all three cultivars tested.

Deren et al. (1991) reported that yields of 160 sugarcane genotypes were reduced by 30 to 100% by 5-mo floods in Florida. This knowledge coupled with reports of acceptable yields of sugarcane under high water tables and short-duration floods suggest that learning more about the physiologic reasons for successful responses of sugarcane to short-duration floods may help identify practices that lengthen the acceptable duration of sugarcane under flood. For example, the roots of all of the >40 sugarcane genotypes examined contained aerenchyma (Ray et al., 1996; Van Der Heyden et al., 1998). Presence of root aerenchyma is a key requisite for sustained root activity in flooded soil.

Stomatal closure, which can reduce carbon assimilation, is a response to flooding that has been noted in other species (Kozlowski, 1997). Stomatal closure in sugarcane that was not provided sufficient water was reported by Saliendra and Meinzer (1991) and Du et al. (1996). Du et al. (1998) further found that stomatal closure in water-deficient sugarcane resulted in reduced P_n . Webster and Eavis (1972) reported that sugarcane T_s was similar for flood and drain treatments until flood duration reached 21 d, after which flooding resulted in reduced T_s . Chabot et al. (2002) did not detect differences in sugarcane T_s due to water-table depths of 5, 20, and 45 cm.

The purpose of this study was to evaluate the effects of periodic flooding followed by drainage to different water-table depths on leaf P_n , T_s , and SC of sugarcane.

It was hoped that this information would further our understanding of the physiologic responses of sugarcane to high water tables and periodic floods so that strategies could be developed in the EAA to sustain sugarcane yields as high water tables and floods increase in occurrence and duration.

MATERIALS AND METHODS

Twelve polyethylene containers equipped as lysimeters were placed into the ground and filled with Pahokee muck soil (Euic, hyperthermic Lithic Haplosaprist). Lysimeters were 1.5 m wide by 2.6 m long by 0.6 m deep and placed where there was no shading. Soil was collected in three arbitrary horizons of 20 cm each. In an attempt to reproduce field bulk densities, the deepest 20-cm horizon of soil was placed in the lysimeters, flooded, and then drained, followed by the next deepest 20-cm layer of soil. The process was continued until the lysimeters were filled. For about three months before planting the first experiment, the soil in the lysimeters underwent cycles of 2-wk flooding followed by drainage for 3 d. Soil bulk densities were not determined at the beginning of this study, but at the conclusion, bulk densities at the 15- and 30-cm depths were 0.29 and 0.21 g cm⁻³, respectively, which were within the range of bulk densities expected of EAA Histosols (Lucas, 1982).

A pump connected to a ball float was installed in each lysimeter to remove excess water. About 40 L of well water entered each lysimeter daily from a hose placed inside a perforated pipe that extended from one corner of the lysimeter above the soil surface to the diagonal corner at the bottom of the lysimeter. A solenoid valve installed on each lysimeter opened automatically once per day for 2 min to permit this water flow. This volume of water was sufficient to return lysimeters to desired water tables each morning if there was a water loss the previous day. Maximum daily water-table reductions during the experiment were 5 cm. Soil samples were taken from the 0- to 15-cm depth and analyzed for pH, P, and K (Sanchez, 1990). On the basis of soil-test recommendations, nutrients were banded near the planted sugarcane each year at rates of 25 and 139 kg ha⁻¹ of P and K, respectively, and at rates of 0.1, 0.1, 0.7, 0.3, 0.1, and 0.3 kg ha⁻¹ of B, Cu, Fe, Mn, Mo, and Zn, respectively.

On 15 May 2000, the lysimeters were drained, and sugarcane was planted in two rows 2.6 m long that were spaced 1.2 m apart. One row in each lysimeter was randomly planted with genotype CP 95-1376 and the other row was planted with genotype CP 95-1429. Both genotypes were previously advanced to the final stage of the Canal Point breeding program based on their high yields and similarity to commercial sugarcane cultivars in Florida. Both years, lysimeters were maintained at water-table depths of 50 cm from after planting until treatments were applied. Three replications of four water-table treatments were imposed the first week of July 2000 and measurements of leaf CO₂ exchange rates (CER) began that week. One treatment that served as a control was a water table-depth that was continuously maintained at 50 cm in three separate lysimeters. The three other water-table treatments, each replicated three times, included flooding for the first 7 d of four 21-d cycles. During the next 14 d of each cycle, these nine lysimeters were maintained at water-table depths of 16, 33, or 50 cm.

The same genotypes were planted in the second experiment on 1 Feb. 2001. Water-table depths in all lysimeters were maintained at 50 cm until 17 Apr. 2001 when the first flood-drain cycle began. Measurements of leaf CER also began

during this flood-drain cycle. Flood-drain cycles each year began when the inter-row space was covered by the plant leaves.

Planting season of sugarcane in Florida extends from August through February, and harvest season from October through April. The experiment in 2000 was planted late because the lysimeters were not ready until May of that year. However, sugarcane is ratooned in Florida, resulting in ratoon crops with wide age differences. The sugarcane from the May planting was similar to the regrowth of a sugarcane field that was harvested in late April. Thus, the timing of flood-drain cycles each year coincided with growth of commercial sugarcane fields in Florida.

Measurements of single-leaf Ps, Ts, SC, and air temperature at the leaf surface were obtained with a CI-301PS Photosynthesis System manufactured by CID, Inc.¹ (CID, Inc. Vancouver, WA) at 2100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density provided to the leaf surface with CID model CI-301LA light source. The CID Photosynthesis System was operated as an open-flow gas exchange system. Leaves measured were those directly below the uppermost fully developed leaf. From each row of each lysimeter, measurements were taken from the middle 11-cm² portion of the leaf area from each of three randomly selected plants not at the end of the row. The flow rate of air through the meter and sample side IRGA was 8.3 mL s⁻¹. Ambient air was used in air flows and CO₂ concentration measured by the system was from 360 to 400 $\mu\text{L L}^{-1}$. Measurement durations were 30 s.

Single-leaf Ps, Ts, and SC were measured for four consecutive flood-drain cycles each year. In 2000, measurements were taken during the first four of five flood-drain cycles. In 2001, when plants were exposed to a total of nine flood-drain cycles, measurements commenced with the first cycle and continued through the fourth cycle. All measurements were taken beginning after dew dried from the leaves (usually about 0900 h) and finished before 1200 h in the first cycle of 2000. We learned during this cycle that Ps, Ts, and SC rates declined substantially on some measurement days for all treatments between 1100 and 1200 h. Declines in Ps that usually occurred later in the day are documented for different species (Schulze and Hall, 1982). Bunce (1990b) found that both high photon flux density and high air saturation-deficits were necessary to cause a diurnal decline in leaf Ps of a C₄ plant such as maize (*Zea mays* L.). For the remainder of the study, measurements were finished before 1100 h, which sometimes required measuring two replications on one day and the third replication the following day. In 2000, measurements were conducted on Day 3, 7, 9, 15, and 21 of each cycle. In 2001, measurements were conducted on Day 7, 11, 17, and 21 of each cycle, except that no measurements were recorded on Day 11 of Cycle 2. Days 1 through 7 were flood days and Days 8 through 21 were drain days both years. Weather information was collected by a weather station located at the experimental site.

The three replications of the four water-table treatments (12 lysimeters) were arranged in a randomized complete block design. Genotypes were arranged as split plots in lysimeters. All statistical analyses were performed by PROC MIXED of SAS (SAS, 1999). Data were analyzed by two procedures. First, to identify treatment effects that were consistently repeated over cycles in each year, the data for each year were analyzed as a split-split plot design with cycles as repeated measures. The first split was genotype and the second split was

measurement day. The second procedure sought to identify treatment effects in individual cycles. To accomplish this, the randomized complete block design of water-table treatments with the split of genotype was analyzed separately for each cycle treating days as repeated measures. On the basis of procedures described by Tao et al. (2002), the unstructured model (type = Un) was used to describe repeated measures covariance in all analyses.

Significant effects identified by analyses of variance were further analyzed by separating least square means with *t* tests. Also, the contrast statement in SAS (SAS, 1999) was used to calculate single degree of freedom comparisons that compared linear regressions of Ps, Ts, or SC on cycles and on days. Differences were identified as significant at $P \leq 0.05$ and as highly significant at $P \leq 0.01$.

RESULTS

Mean daily air temperatures during the course of this study were 26.5°C in 2000 and 24.7°C in 2001. The higher temperatures in 2000 were expected because measurements in that experiment began in July compared with April in 2001. Maximum and minimum daily temperatures were less variable in 2000 than in 2001 (Fig. 1). Standard deviations of maximum temperatures were 2.0 and 2.6°C in 2000 and 2001, respectively; and standard deviations of minimum temperatures were 1.6 and 2.7°C in 2000 and 2001, respectively. Within measurement days, there were no significant differences in air temperature at the leaf due to genotype or water treatment for any cycle in either year (data not shown).

Analyses of Ps, Ts, and SC repeated over cycles detected significant differences in Ts and SC due to water treatment in 2001, but not in 2000 (Table 1). Water treatment did not interact significantly with any other treatment in the analyses repeated over cycles. Transpiration in the constant 50-cm water table (control) was similar to Ts in the treatments that were flooded and drained to 50 and 33 cm in 2001, but less than that of the periodically flooded treatment that was maintained at a 16-cm water-table depth during drain periods (Table 2). Among treatments that were periodically flooded, Ts in the treatment that was drained to 16 cm was greater than in the treatment drained to 33 cm. In 2001, SC in the water table that was maintained continuously at 50 cm was similar to the SC rates of the three water treatments that were periodically flooded. Of the three treatments that were periodically flooded, SC was highest in the treatment maintained at 16 cm during drainage.

Highly significant differences in Ts and SC were detected between the two genotypes in 2000 (Table 1). Higher rates of Ts and SC were measured in CP 95-1429 than in CP 95-1376 in 2000 (Table 3). In 2001, the Ps of CP 95-1376 was significantly higher than that of CP 95-1429 and the Ts and SC of CP 95-1376 were almost significantly higher than the Ts and SC of CP 95-1429. There were no significant interactions involving genotype in the analyses repeated over cycles.

The cane and sugar yields of CP 95-1376 were significantly greater than those of CP 95-1429 both years (Glaz et al., 2004). Thus, it was expected that CER of CP 95-1376 would be higher than those of CP 95-1429 both

¹ Mention of trade names or commercial products is solely for the purpose of providing specific information and does not imply recommendation or endorsement by USDA or the University of Florida over others not mentioned.

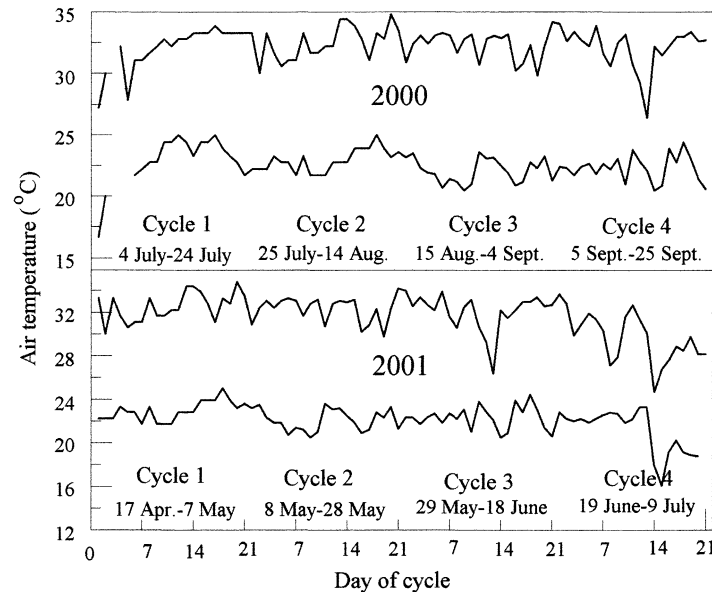


Fig. 1. Minimum and maximum air temperatures when sugarcane leaf-photosynthesis measurements were conducted at Canal Point, FL, in 2000 and 2001.

years. The probable cause of the higher leaf Ts and SC for CP 95-1429 in 2000 was its low plant population. In 2000, mean stalks per meter at harvest were 6.8 for CP 95-1429 compared with 16.4 for CP 95-1376. In 2001, when Ps of CP 95-1376 was higher than that of CP 95-1429, the difference in stalk number between the two genotypes narrowed; the stalks per meter of CP 95-1429 improved to 10.5 compared with 15.8 for CP 95-1376. This explanation is supported by Bunce (1990a) who reported that as plant density increased in maize field plots with a 1.5-m water-table depth, leaf Ps declined, probably because of increased mutual shading among leaves, and perhaps greater water deficits. Water deficits probably did not play a role in the present study because

water tables ranged from flood to 50 cm below the soil surface.

Measurement day and cycle and their interactions were highly significant for all three characters in both years (Table 1). Significant differences among cycles were probably due to growth stage of the plants or to weather conditions. Differences among days were also probably related to changes in weather conditions and to a lesser extent, to growth stage of the plant. However, a controlled condition that was confounded with days was flood-drain status. Three treatments were flooded on Days 1 through 7, and drained to their designated depths on Days 8 through 21 of each cycle. To determine whether flood-drain status may have partially caused

Table 1. Probabilities of *F* values of fixed effects for single-leaf net photosynthetic rate (Ps), transpiration (Ts), and stomatal conductance (SC) from measurements repeated over cycles in 2000 and 2001.

Fixed effect	Year		2000			2001		
	2000	2001	Ps	Ts	SC	Ps	Ts	SC
	df		<i>P</i> > <i>F</i>					
Water treatment (W)	3	3	0.36	0.41	0.38	0.43	0.03	0.03
Genotype (G)	1	1	0.34	0.01	0.01	0.05	0.06	0.07
W × G	3	3	0.46	0.96	0.96	0.15	0.49	0.59
Day (D)	4	3	<0.01	<0.01	<0.01	<0.01	<0.01	0.01
D × W	12	9	0.73	0.62	0.75	0.27	0.51	0.19
D × G	4	3	0.72	0.39	0.60	0.60	0.28	0.42
D × W × G	12	9	0.81	0.56	0.39	0.57	0.71	0.25
Cycle (C)	3	3	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
C × W	9	9	0.62	0.31	0.37	0.65	0.75	0.56
C × G	3	3	0.92	0.32	0.45	0.12	0.11	0.25
C × W × G	9	9	0.42	0.69	0.54	0.54	0.54	0.07
C × D	12	9	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
C1 vs. C2 × D linear†	1	1	0.15	0.25	0.08	0.04	<0.01	0.03
C1 vs. C3 × D linear	1	1	0.97	0.98	0.25	0.10	<0.01	<0.01
C1 vs. C4 × D linear	1	1	0.01	0.01	0.10	0.10	0.03	0.02
C2 vs. C3 × D linear	1	1	0.05	0.05	0.10	0.90	0.74	0.08
C2 vs. C4 × D linear	1	1	<0.01	<0.01	<0.01	0.75	0.20	0.18
C3 vs. C4 × D linear	1	1	<0.01	<0.01	<0.01	0.68	0.53	0.05
C × D × W	36	27	0.08	0.48	0.43	0.29	0.54	0.06
C × D × G	12	9	0.62	0.52	0.99	0.95	0.83	0.89
C × D × W × G	36	27	0.68	0.37	0.96	0.64	0.93	0.98

† Linear effect of Cycle 1 regressed on days compared with linear effect of Cycle 2 regressed on days. Similar explanations for other single degree of freedom interactions.

Table 2. Leaf photosynthesis, transpiration, and stomatal conductance least square means of four water-table treatments in 2000 and 2001.

Treatment†	Year	Photosynthesis	Transpiration	Stomatal conductance
		$\mu\text{mol m}^{-2} \text{s}^{-1}$	$\text{mmol m}^{-2} \text{s}^{-1}$	
50 always	2000	7.20 a‡	0.36 a	15.79 a
16 & flood	2000	8.09 a	0.42 a	19.19 a
33 & flood	2000	8.57 a	0.45 a	21.42 a
50 & flood	2000	8.14 a	0.36 a	16.73 a
Mean	2000	8.00	0.40	18.28
50 always	2001	8.94 a	0.39 b	21.65 ab
16 & flood	2001	9.88 a	0.50 a	26.64 a
33 & flood	2001	8.44 a	0.38 b	18.14 b
50 & flood	2001	9.44 a	0.43 ab	21.04 b
Mean	2001	9.18	0.43	21.87

† Treatments were water-table depths of 50-cm always and cycles of flood for 7 d followed by depths of 16, 33, and 50 cm for 14 d for 4 cycles in 2000 and 2001, respectively.

‡ Least square means in the same column and year followed by the same letter are not significantly different ($P = 0.05$) based on t tests.

the day \times cycle interactions, linear responses of Ps, Ts, and SC of each cycle were regressed on measurement day (Fig. 2). In 2000, highly significant interactions were identified for the linear responses of Cycles 1, 2, and 3 on day when compared with those of Cycle 4 for all characters except for the SC responses of Cycles 1 and 4 (Table 1 and Fig. 2). One interpretation of these interactions is that flooding either improved or did not affect CER in Cycles 1 through 3 of 2000, but flooding reduced CER in Cycle 4.

In 2001, the linear responses of Cycles 2, 3, and 4 on Day differed from those of Cycle 1 for Ts and SC (Table 1). These significant interactions suggest that flooding improved Ts and SC in Cycle 1, but did not affect Ts or SC in Cycles 2 through 4. These inconsistent results between 2000 and 2001 suggest that rather than flood-drain status, differences in growth stage and

Table 3. Leaf photosynthesis, transpiration, and stomatal conductance least square means of two sugarcane genotypes in 2000 and 2001.

Genotype	Year	Photosynthesis	Transpiration	Stomatal conductance
		$\mu\text{mol m}^{-2} \text{s}^{-1}$	$\text{mmol m}^{-2} \text{s}^{-1}$	
CP 95-1376	2000	8.13	0.38	17.27
CP 95-1429	2000	7.87	0.42	19.30
$P > t$	2000	0.34	0.01	0.01
CP 95-1376	2001	9.58	0.46	23.21
CP 95-1429	2001	8.88	0.41	20.53
$P > t$	2001	0.05	0.06	0.07

weather were the major causes of the significant cycle \times day interactions.

As cycles progressed each year, Ps, Ts, and SC declined, particularly during flooding (Fig. 2). Except for Ps in 2001, all three characters declined linearly over cycles both years ($P < 0.01$). Increased tiller number related to increased plant age may have been one cause of these declining rates with cycles. A second possible cause is that the repeated floods may have had cumulative negative effects on sugarcane CER. To test the second hypothesis, the linear response on cycles of the control treatment was compared with the mean linear response on cycles of the three flooding treatments for each flood day. No interaction was significant in 2000 or 2001 (data not shown) suggesting that the repeated flooding was not detrimental to sugarcane CER.

Analyses of each year with cycles as repeated measures resulted in two clear conclusions. First, exposure to four 21-d cycles of 7-d flooding followed by 14-d drainage did not reduce sugarcane Ps, Ts, or SC on flood days. Second, 7-d flooding followed by 14-d drainage to 16 cm usually resulted in equal, but occasionally higher, sugarcane leaf CER than the control or 7-d flooding drained to water-table depths of 33 or 50 cm. Analyses

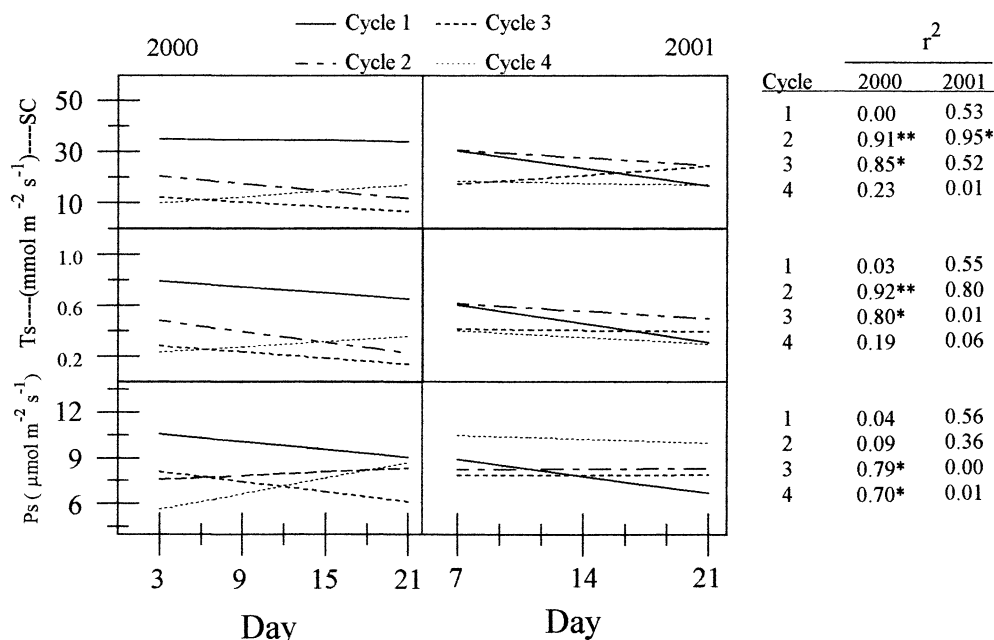


Fig. 2. Leaf photosynthesis (Ps), transpiration (Ts), and stomatal conductance (SC) of four 21-d water-management cycles regressed on measurement days in 2000 and 2001. * and ** represent significance of r^2 values at the 0.05 and 0.01 levels, respectively.

Table 4. Probabilities of significant *F* values, by cycle, of fixed effects for leaf photosynthesis (Ps), transpiration (Ts), and stomatal conductance (SC) measurements repeated over days in 2000 and 2001.

Cycle	Fixed effect	Year 2000			Year 2001		
		Ps	Ts	SC	Ps	Ts	SC
		<i>P</i> > <i>F</i>					
1	Water	0.70	0.89	0.53	0.85	0.94	0.70
1	Genotype	0.82	0.30	0.32	0.02	<0.01	<0.01
1	Water × genotype	0.89	0.96	0.98	0.09	0.07	0.07
1	Day	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
1	Water × day	0.23	0.43	0.78	0.01	0.03	0.10
1	Genotype × day	0.35	0.88	0.95	0.11	0.15	0.65
1	Water × genotype × day	0.16	0.45	0.26	0.28	0.64	0.48
2	Water	0.79	0.91	0.90	0.41	0.38	0.36
2	Genotype	0.66	0.17	0.33	0.88	0.05	0.18
2	Water × genotype	0.70	0.86	0.77	0.17	0.18	0.15
2	Day	<0.01	0.01	0.01	0.54	0.19	0.07
2	Water × day	0.23	0.73	0.43	0.44	0.36	0.12
2	Genotype × day	0.60	0.10	0.07	0.82	0.11	0.21
2	Water × genotype × day	0.50	0.79	0.65	0.61	0.70	0.40
3	Water	0.01	0.07	0.41	0.50	0.03	<0.01
3	Genotype	0.23	0.17	0.61	0.87	0.90	0.65
3	Water × genotype	0.26	0.36	0.77	0.89	0.53	0.12
3	Day	<0.01	<0.01	<0.01	0.22	<0.01	0.01
3	Water × day	0.28	0.78	0.08	0.68	0.64	0.39
3	Genotype × day	0.45	0.65	0.41	0.84	0.79	0.97
3	Water × genotype × day	0.80	0.30	0.43	0.89	0.64	0.79
4	Water	0.39	0.07	0.05	0.01	0.02	0.01
4	Genotype	0.49	0.17	0.42	0.07	0.76	0.09
4	Water × genotype	0.50	0.36	0.89	0.71	0.76	0.70
4	Day	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
4	Water × day	0.44	0.78	0.67	0.64	0.15	0.06
4	Genotype × day	0.99	0.65	0.95	0.88	0.54	0.86
4	Water × genotype × day	0.39	0.30	0.75	0.98	0.61	0.45

were then conducted on each cycle with days as repeated measures to verify that the mean results of each year were not masking negative effects of flood or high water tables on sugarcane CER rates (Table 4). These analyses confirmed that within cycles, measurement day was the treatment that most consistently resulted in significant effects on Ps, Ts, and SC. The lack of significance among days in Cycle 2 of 2001 is probably because measurements were obtained for 3 rather than 4 d in that cycle.

In Cycle 3, water treatments significantly affected Ps in 2000 and Ts and SC in 2001 (Table 4). In 2000, Ps in the control treatment was lower than in all three treatments that were periodically flooded for 7 d (Table 5). In Cycle 3 of 2001, Ts in the water-table depth main-

tained at 16 cm during drain periods was significantly greater than at 33 cm, and the SC at 16 cm was significantly greater than SC of all other water-table treatments.

In Cycle 4, water treatments significantly affected SC in Year 2000 and Ps, Ts, and SC in Year 2001 (Table 4). In 2000, the cause of the significant difference was that SC of the water table that was flooded for 7 d and drained to 33 cm for 14 d was higher than that of the control and higher than that of the water table that was flooded and maintained at 50 cm during drainage (Table 4). In 2000, the overall *F* test in Cycle 4 for Ts was not significant, but similar treatment differences were identified by *t* tests (Tables 4 and 5). When significant differences have been identified among water treat-

Table 5. Least square means of single-leaf photosynthesis (Ps), transpiration (Ts), and stomatal conductance (SC) rates of water-table treatments for years and cycles in which water treatment was identified as significant by analysis of variance for Ps, Ts, or SC.

Year	Cycle	Water treatment and depth†	Ps	Ts	SC
			$\mu\text{mol m}^{-2} \text{s}^{-1}$	$\text{mmol m}^{-2} \text{s}^{-1}$	
2000	3	Constant 50 cm	6.21 b‡	0.15 a	6.62 a
2000	3	7-d flood, 14 d at 16 cm	7.23 a	0.22 a	9.56 a
2000	3	7-d flood, 14 d at 33 cm	7.98 a	0.31 a	7.46 a
2000	3	7-d flood, 14 d at 50 cm	7.42 a	0.17 a	13.50 a
2000	4	Constant 50 cm	6.04 a	0.24 b	10.22 b
2000	4	7-d flood, 14 d at 16 cm	7.19 a	0.32 ab	14.53 ab
2000	4	7-d flood, 14 d at 33 cm	7.68 a	0.36 a	16.81 a
2000	4	7-d flood, 14 d at 50 cm	6.99 a	0.22 b	10.02 b
2001	3	Constant 50 cm	8.26 a	0.40 ab	21.17 b
2001	3	7-d flood, 14 d at 16 cm	9.57 a	0.49 a	27.77 a
2001	3	7-d flood, 14 d at 33 cm	7.56 a	0.28 c	15.55 b
2001	3	7-d flood, 14 d at 50 cm	8.99 a	0.38 abc	17.83 b
2001	4	Constant 50 cm	10.16 b	0.32 b	16.25 b
2001	4	7-d flood, 14 d at 16 cm	11.69 a	0.44 a	24.30 a
2001	4	7-d flood, 14 d at 33 cm	9.80 b	0.28 b	12.59 b
2001	4	7-d flood, 14 d at 50 cm	10.74 ab	0.34 b	16.67 b

† Water-table treatments were maintained at 50 cm throughout the study or flooded for 7 d, followed by drainage to depths of 16, 33, and 50 cm for 14 d. These 21-d cycles were repeated four times each year.

‡ Least square means in the same column, year, and cycle followed by the same letter are not significantly different ($P = 0.05$) based on *t* tests.

Table 6. Least square means of single-leaf photosynthesis (Ps) and transpiration (Ts) rates of four water-table treatments for 5 d during the first of four flood-drain cycles in 2001.

Water treatment and depth†	Cycle day	Ps	Ts
		$\mu\text{mol m}^{-2} \text{s}^{-1}$	$\text{mmol m}^{-2} \text{s}^{-1}$
Constant 50 cm	7	12.36 a‡	0.84 a
7-d flood, 14 d at 16 cm	7	10.52 ab	0.88 a
7-d flood, 14 d at 33 cm	7	8.02 b	0.58 a
7-d flood, 14 d at 50 cm	7	9.47 ab	0.77 a
Constant 50 cm	11	8.26 ab	0.28 a
7-d flood, 14 d at 16 cm	11	6.35 b	0.36 a
7-d flood, 14 d at 33 cm	11	8.78 a	0.51 a
7-d flood, 14 d at 50 cm	11	7.56 ab	0.33 a
Constant 50 cm	17	8.70 a	0.57 a
7-d flood, 14 d at 16 cm	17	7.99 a	0.49 a
7-d flood, 14 d at 33 cm	17	7.85 a	0.34 a
7-d flood, 14 d at 50 cm	17	9.18 a	0.53 a
Constant 50 cm	21	6.38 a	0.21 a
7-d flood, 14 d at 16 cm	21	7.10 a	0.30 a
7-d flood, 14 d at 33 cm	21	9.01 a	0.41 a
7-d flood, 14 d at 50 cm	21	7.21 a	0.27 a

† Water-table treatments were maintained at 50 cm throughout the study or flooded for 7 d, followed by drainage to depths of 16, 33, and 50 cm for 14 d. These 21-d cycles were repeated four times each year.

‡ Least square means in the same column and day followed by the same letter are not significantly different ($P = 0.05$) based on t tests.

ments in most other instances of this study, it has been the periodically flooded treatment drained to a depth of 16, rather than 33 cm, that has been the favorable treatment.

In Cycle 4 of Year 2001, the periodically flooded treatment maintained at 16 cm during drainage had higher Ts and SC than all other treatments. Results were similar for Ps except that the periodically flooded treatments maintained at 16 and 50 cm during drainage had similar Ps rates. These responses were similar to the mean responses of Ts and SC over all cycles in 2001 (Table 2).

In Cycle 1 of Year 2001, the interactions of water treatment \times day were significant for Ps and Ts (Table 4). Linear regressions of water-table depth during drainage for periodically flooded treatments did not explain these significant interactions (data not shown). Therefore, the means were separated by t tests (Table 6). The control treatment had higher Ps on Day 7 than the periodically flooded treatment maintained at a water-table depth of 33 cm during drainage. On Day 11, drainage to 33 cm resulted in higher Ps than drainage to 16 cm. Except for this and one other instance in this study, for treatments that were periodically flooded, drainage to 16 cm resulted in CER rates greater than or equal to drainage to 33 cm. All water-table treatments had similar Ps and Ts on Days 17 and 21.

DISCUSSION

The rates of Ps, Ts, and SC measured in this study (mean Ps = $8.6 \mu\text{mol m}^{-2} \text{s}^{-1}$) were lower than rates reported elsewhere for C_4 species. Nilsen and Orcutt (1996) reported a Ps rate generalized for a large number of C_4 species exposed to high light of about $20 \mu\text{mol m}^{-2} \text{s}^{-1}$. At normal ambient air CO_2 concentrations and leaf N concentrations, for sugarcane planted in pots at low plant densities in greenhouses, Ps rates of $>30 \mu\text{mol m}^{-2} \text{s}^{-1}$ were reported at Gainesville, FL (about

400 km north of the EAA) (Vu et al., 2001) and Hawaii (Meinzer and Zhu, 1998). Sugarcane Ps rates similar to those we measured were reported by Meinzer and Zhu (1998) when leaf N concentrations dropped below about 40 mmol m^{-2} and by Du et al. (1996) when leaf water potential approached -0.80 MPa .

Bunce (1990a) reported that as densities increased from 4 to 20 plants m^{-2} , Ps of maize declined from 45 to $32 \mu\text{mol m}^{-2} \text{s}^{-1}$. Sugarcane tillers profusely during the summer in Florida; stalk densities approximated 45 to 50 stalks m^{-2} during our measurement periods and later declined to levels of about 6 to 16 stalks m^{-2} by harvest. In hundreds of measurements of young sugarcane leaves growing at densities <10 stalks m^{-2} in pots at Canal Point, FL, Ps averaged about $20 \mu\text{mol m}^{-2} \text{s}^{-1}$. As sugarcane tillers in these pots increased, Ps rates dropped to about $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Glaz, unpublished data, 2003). Thus, plant density partially explains the low Ps, Ts, and SC reported here compared with other reports. It is not known if other factors reduced our measured CER rates, but these rates were measured consistently throughout this 2-yr study, were similar to rates of sugarcane growing in the field under similar plant densities, and were verified with a second instrument.

This 2-yr study, with four 21-d cycles each year, and five (Year 2000) and four (Year 2001) measurement days in cycles showed that four periodic 7-d floods either do not affect or moderately enhance Ps, Ts, and SC of sugarcane. This result supports the finding of Webster and Eavis (1972) that Ts did not decrease until sugarcane was flooded for 21 d. Unlike for some other species, our results lead to the conclusion that floods of up to 7 d did not cause stomatal closure that would reduce either Ts or Ps of sugarcane. A general conclusion is that several 7-d floods during the summer growing season would not reduce sugarcane yields due to reduced Ps. Perhaps the presence of aerenchyma in sugarcane is partially responsible for avoiding stomatal closure during 7-d floods.

The combination of neutral and favorable responses to 7-d floods suggests that under some conditions flooding may even enhance sugarcane Ps. Early in the study, we found that sugarcane Ps, Ts, and SC all declined sharply shortly before noon. On the basis of these early results, we rearranged schedules to assure that all measurements were concluded by 1100 h. Bunce (1990b) found that in the presence of high photon flux density, high air saturation-deficits caused declines in leaf Ps of maize. Perhaps by maintaining its hydration, flood and high water tables help sugarcane maintain optimum Ps longer under these late morning conditions. This speculation identifies a needed research area.

In the second year of the study, four 21-d cycles, each with 7 consecutive days flood, resulted in higher sugarcane Ts and SC rates when drained to a depth of 16 compared with 33 cm (Table 2). A similar response was identified for Ps in the final cycle of 2001 (Table 5). These analyses also identified favorable results for the periodically flooded treatment drained to 16 cm compared with the control and the periodically flooded

treatment drained to 50 cm. Thus, it can be concluded that draining to 16 cm after exposures to 7-d flooding either does not affect or enhances sugarcane Ps, Ts, and SC.

Fresh weight cane yields of CP 95-1376 (21.85 g m⁻² in 2000 and 25.46 g m⁻² in 2001) were greater than those of CP 95-1429 (9.05 g m⁻² in 2000 and 23.30 g m⁻² in 2001). Periodic flooding and drainage to increasingly shallow water-table depths significantly reduced yields in CP 95-1376, but not in CP 95-1429 (Glaz et al., 2004). In species that are flood tolerant, aerenchyma formation is usually constitutive, meaning that it requires no external stimulus, such as flood (Drew, 1997). It was discovered that CP 95-1429 had constitutive stalk aerenchyma, but aerenchyma formed only in stalks of CP 95-1376 after they were exposed to flooding (Glaz et al., 2004).

The water × genotype interaction was not significant throughout this study (Tables 1 and 4). However, with the knowledge that CP 95-1429 had constitutive stalk aerenchyma and CP 95-1376 only formed stalk aerenchyma after flooding, the Ps in the control for each genotype was compared with the mean Ps of the flood-drain treatments on flood days. No significant differences between these two treatments were identified for CP 95-1429 Ps rates (data not shown), thus supporting the conclusion that it had constitutive stalk aerenchyma. CP 95-1376 had similar Ps rates in flooded and drained plants during flood measurement days of Cycle 1 in 2000 (data not shown). However, in Cycle 1, Day 7 of 2001, Ps of CP 95-1376 was significantly higher ($P = 0.03$) in the drained than in the flooded plants (15.0 μmol m⁻² s⁻¹ vs. 9.3 μmol m⁻² s⁻¹). No differences between drained and flooded CP 95-1376 Ps were identified in later cycles.

It is possible that after the first cycle in 2001, CP 95-1376 plants that were flooded formed stalk aerenchyma which enabled plants to sustain optimum Ps, Ts, and SC rates during the 7-d flooding for the remaining three cycles. In both years of this study, CP 95-1376 plants subjected to periodic flooding had stalk aerenchyma when examined at harvest, and those not flooded did not have stalk aerenchyma (Glaz et al., 2004). Perhaps it was a delay in aerenchyma formation until after flooding (both years) and the subsequently reduced Ps rates during Cycle 1 of 2001 that caused yield losses in CP 95-1376 flooding treatments. Aerenchyma formation after Cycle 1 would explain why Ps, Ts, and SC rates of CP 95-1376 did not decline because of flood or high water table after Cycle 1. Further research is needed to verify if the ability to form constitutive stalk aerenchyma affects Ps during the first exposure of sugarcane to flooding.

If later research verifies differences in yield response to flood because of the presence or absence of constitutive stalk aerenchyma, this information could help farm managers maintain high yields in sugarcane exposed to periodic floods. For cultivars that need exposure to flood to form aerenchyma, perhaps a first flood exposure could be managed to be of short duration (but long enough to cause aerenchyma formation) and then later flood durations could be longer after stalk aerenchyma are present. For this option to sustain high yields, it

would be necessary to identify high yielding cultivars whose yields are not compromised by aerenchyma formation. A second option would be to develop high yielding cultivars that form constitutive stalk aerenchyma.

The report of Glaz et al. (2002) of 25% yield losses due to field water-table depths of <15 cm compared with 15 to 38 cm suggests that sugarcane Ps may decline if nonflooded water tables are <15 cm for long durations. Further studies on the effects of water table on sugarcane Ps, Ts, and SC should determine a detailed response curve for water tables between 0 and 33 cm. Also needed is a study that determines the effects of flood durations longer than 7 d on sugarcane Ps, Ts, and SC.

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REFERENCES

- Bunce, J.A. 1990a. Afternoon inhibition of photosynthesis in maize. 1. Evidence, and relationship to stand density. *Field Crops Res.* 24:251–260.
- Bunce, J.A. 1990b. Afternoon inhibition of photosynthesis in maize. 2. Environmental causes and physiological symptoms. *Field Crops Res.* 24:261–271.
- Carter, C.E., and J.M. Floyd. 1971. Effects of water table depths on sugarcane yields in Louisiana. *Proc. Am. Soc. Sugar Cane Technol.* 2:5–7.
- Carter, C.E., and J.M. Floyd. 1975. Inhibition of sugarcane yields by high water table during dormant season. *Proc. Am. Soc. Sugar Cane Technol.* 4:14–18.
- Chabot, R., S. Bouarfa, D. Zimmer, C. Chaumont, and C. Duprez. 2002. Sugarcane transpiration with shallow water-table: Sap flow measurements and modelling. *Agric. Water Manage.* 54:17–36.
- Deren, C.W., G.H. Snyder, J.D. Miller, and P.S. Porter. 1991. Screening for and heritability of flood-tolerance in the Florida (CP) sugarcane breeding population. *Euphytica* 56:155–160.
- Drew, M.C. 1997. Oxygen deficiency and root metabolism: Injury and acclimation under hypoxia and anoxia. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 48:223–250.
- Du, Y.C., Y. Kawamitsu, A. Nose, S. Hiyane, S. Murayama, K. Wasano, and Y. Uchida. 1996. Effects of water stress on carbon exchange rate and activities of photosynthetic enzymes in leaves of sugarcane (*Saccharum* sp.). *Aust. J. Plant Physiol.* 23:719–726.
- Du, Y.C., A. Nose, K. Wasano, and Y. Uchida. 1998. Responses to water stress of enzyme activities and metabolite levels in relation to sucrose and starch synthesis, the Calvin cycle and the C-4 pathway in sugarcane (*Saccharum* sp.) leaves. *J. Plant Physiol.* 25: 253–260.
- Gascho, G.J., and S.F. Shih. 1979. Varietal response of sugarcane to water table depth. 1. Lysimeter performance and plant response. *Soil Crop Sci. Soc. Fla. Proc.* 38:23–27.
- Glaz, B. 2002. Sugarcane variety census: Florida 2001. *Sugar J.* 65(3): 35–39.
- Glaz, B., S.J. Edme, J.D. Miller, S.B. Milligan, and D.G. Holder. 2002. Sugarcane cultivar response to high summer water tables in the Everglades. *Agron. J.* 94:624–629.
- Glaz, B., D.R. Morris, and S.H. Daroub. 2004. Periodic flooding and water table effects on two sugarcane genotypes. *Agron. J.* 96:832–838.
- Kang, M.S., G.H. Snyder, and J.D. Miller. 1986. Evaluation of *Saccharum* and related germplasm for tolerance to high water table on organic soil. *J. Am. Soc. Sugar Cane Technol.* 6:59–63.
- Kozlowski, T.T. 1997. Responses of woody plants to flooding and salinity. *Tree physiology monogr.* 1. Heron Publishing, Victoria, BC, Canada.
- Lucas, R.E. 1982. Organic soils (Histosols) formation, distribution,

- physical and chemical properties and management for crop production. Res. Report 435. Mich. State Univ. East Lansing, MI.
- Mafizur Rahman, A.B.M., F.A. Martin, and M.E. Terry. 1986. Growth responses of *Saccharum* spp to flooding. p. 236–244. In J.L. Clayton and H. Handojo (ed.) 1986. Int. Soc. Sugar Cane Technol: Proc. XIX Congress, Vol. 1, Jakarta, Indonesia. 21–31 August 1986.
- Meinzer, F.C., and J. Zhu. 1998. Nitrogen stress reduces the efficiency of the C₄ CO₂ concentrating system, and therefore quantum yield, in *Saccharum* (sugarcane) species. J. Exp. Bot. 49:1227–1234.
- Nilsen, E.T., and D.M. Orcutt. 1996. The physiology of plants under stress. John Wiley & Sons, New York.
- Omary, M., and F.T. Izuno. 1995. Evaluation of sugarcane evapotranspiration from water table data in the everglades agricultural area. Agric. Water Manage. 27:309–319.
- Ray, J.D., J.D. Miller, and T.R. Sinclair. 1996. Survey of aerenchyma in sugarcane roots. p. 118. In Fifth Symposium, Int. Soc. of Root Research. July 14–18, 1996. Clemson, SC.
- Rice, R.W., F.T. Izuno, and R.M. Garcia. 2002. Phosphorus load reductions under best management practices for sugarcane cropping systems in the Everglades Agricultural Area. Agric. Water Manage. 56:17–39.
- Saliendra, N.Z., and F.C. Meinzer. 1991. Symplast volume, turgor, stomatal conductance and growth in relation to osmotic and elastic adjustment in droughted sugarcane. J. Exp. Bot. 42(243):1251–1259.
- Sanchez, C.A. 1990. Soil-testing and fertilization recommendations for crop production on organic soils in Florida. Bull. 87. University of Florida, Gainesville.
- SAS. 1999. SAS system for Windows release 8.2. SAS Inst., Cary, NC.
- Schulze, E.-D., and A.E. Hall. 1982. Stomatal responses, water loss and CO₂ assimilation rates of plants in contrasting environments. p. 181–230. In O.L. Lange et al. (ed.) Physiological plant ecology II. Water relations and carbon assimilation. Springer, New York.
- Shih, S.F., B. Glaz, and R.E. Barnes, Jr. 1998. Subsidence of organic soils in the Everglades Agricultural Area during the past 19 years. Soil Crop Sci. Soc. Fla. Proc. 57:20–29.
- Shih, S.F., and E.H. Stewart, Jr. L. H. Allen, and J. W. Hilliard. 1978. Variability of depth to bedrock in Everglades organic soil. Soil Crop Sci. Soc. Fla. Proc. 38:66–71.
- Snyder, G.H., H.W. Burdine, J.R. Crockett, G.J. Gascho, D.S. Harrison, G. Kidder, J.W. Mishoe, D.L. Myhre, F.M. Pate, and S.F. Shih. 1978. Water table management for organic soil conservation and crop production in the Florida Everglades. Bull. 801. Agric. Exp. Stn., Institute of Food and Agricultural Sciences, University of Florida, Gainesville.
- Snyder, G.H., and J.M. Davidson. 1994. Everglades agriculture, past, present, and future. In S.M. Davis and J.C. Ogden (ed.) Everglades: The ecosystem and its restoration. St. Lucie Press, Delray Beach, FL.
- Tao, J., R. Littell, M. Patetta, C. Truxillo, and R. Wolfinger. 2002. Mixed models analyses using the SAS system: Course notes. SAS Institute, Inc., Cary, NC.
- Tate, R.L., III. 1980. Microbial oxidation of organic matter of Histo-sols. Adv. Microb. Ecol. 4:169–201.
- Van Der Heyden, C., J.D. Ray, and R. Nable. 1998. Effects of water-logging on young sugarcane plants. Aust. Sugarcane 2:28–30.
- Vu, J.C., L.H. Allen, Jr., and M. Gallo-Meagher. 2001. Crop plant responses to rising CO₂ and climate change. In M. Pessaraki (ed.) Handbook of plant and crop physiology: Second edition revised and expanded. Marcel Dekker, New York.
- Webster, P.W.D., and B.W. Eavis. 1972. Effects of flooding on sugarcane growth. 1. Stage of growth and duration of flooding. p. 708–714. In M.T. Henderson (ed.) Proc. Int. Soc. Sugar Cane Technol. Fourteenth Congress, 22 Oct.–5 Nov. 1971. New Orleans, LA.