Root-zone Sodium Chloride Influences Photosynthesis, Water Relations, and Mineral Content of Sapodilla Foliage

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Additional index words. chlorophyll fluorescence, *Manilkara zapota*, net CO₂ assimilation

Abstract. Sapodilla [*Manilkara zapota* (L.) Royen], reportedly tolerant of saline conditions relative to other tropical fruit species, was studied in sand culture under greenhouse conditions to examine the physiology of sapodilla trees exposed to NaCl and to aid in determining the basis for this apparent tolerance. Treatments, consisting of a complete nutrient solution of 1 dS·m⁻¹ (control) or this solution amended to 12 or 20 dS·m⁻¹ with NaCl, were administered from 16 Nov. 1991 until 29 Jan. 1992. Net CO₂ assimilation (A) of plants receiving NaCl gradually decreased relative to that of the control plants. At the end of 8 weeks of salinity, A of plants receiving 12 or 20 dS·m⁻¹ was 72% or 31% of control plants, respectively. Substrate NaCl reduced apparent quantum yield, photosynthetic CO₂-use efficiency, leaf osmotic potential, and predawn xylem potential of sapodilla leaves. Dark respiration and the variable : maximal chlorophyll fluorescence ratio were not influenced by NaCl. Exposure to NaCl also increased leaf tissue Na⁺ and Cl⁻ concentrations and the Na⁺: K⁺ ratio. These results indicate that gas exchange of sapodilla is relatively low for woody evergreen species. Moreover, sapodilla may not be as tolerant of salt stress as previously reported. The responses of sapodilla to root zone NaCl were consistent with other woody perennial glycophyte species. Photochemical efficiency of leaves on plants receiving NaCl was not different from that of leaves on control plants for >8 weeks after NaCl reduced gas exchange.

Sapodilla is an important woody perennial fruit species that is grown throughout the tropics for its beauty as a landscape specimen, tolerance of harsh conditions, and fruit production. Total sapodilla production amounts to 12,000 ha worldwide, with the bulk of production in the Philippines, India, Mexico, Malaysia, and Venezuela (International Board for Plant Genetic Resources, 1986; Rowe-Dutton, 1976). Sapodilla trees were the source of chicle, the main ingredient in chewing gum, for many years and much of the cultivation in Mexico is still for this product (Lakshminarayana, 1980).

Salinity is a worldwide agricultural problem, including in the lowland tropical coastal areas where sapodilla is commonly grown. In these areas, high salt levels may influence plants through saltwater intrusion into ground water and through wind-borne salt (Maas, 1994). Patil and Patil (1983) reported that sapodilla was tolerant of root-zone salt levels ≤12 dS·m⁻¹ [electrical conductivity (EC) of the soil saturation extract (EC_e)]. This report was based on the influence of 19 months of exposure to salinity on vegetative growth of young seedlings. Their results indicate that sapodilla is tolerant or moderately tolerant of salinity

based on the criteria of Maas and Hoffman (1977) and is highly tolerant relative to other tropical fruit species. Sapodilla also is reported to be tolerant of salt spray (International Board for Plant Genetic Resources, 1986).

Mineral absorption and physiological responses of sapodilla to substrate NaCl have not been determined. Moreover, to our knowledge, there have been no reports providing the photosynthetic characteristics of sapodilla leaves under nonstress conditions or in response to changes in environmental variables. Our study was undertaken to determine the foliar gas exchange, water relations, chlorophyll fluorescence, and mineral content of sapodilla plants exposed to nutrient solutions containing NaCl for the purpose of determining the basis for the unusually high level of tolerance reported for this tropical fruit species.

Materials and Methods

Seeds of 'Prolific' sapodilla were planted in Mar. 1990 in a whitewashed glasshouse under 50% ambient light. The seedlings were maintained in a container nursery setting until 5 Aug. 1991. Seedlings were transplanted into silica sand in 2.6-liter containers and were moved to a polypropylene greenhouse where maximum photosynthetic photon flux (PPF) was 2250 μmol·m⁻²·s⁻¹. Plants were watered daily with complete nutrient solution consisting of 0.62 g Hydro-sol (W.R. Grace & Co., Fogelsville, Pa.) and 0.41 g Ca(NO₃)₂/liter.

This solution had a pH of ≈7.0 and an EC of 1 dS·m⁻¹. This balanced nutrient solution approximated 45% of full-strength Hoagland solution (Hoagland and Arnon, 1950).

Treatments consisted of nutrient solutions with EC of 1 (control), 12, or 20 dS·m⁻¹, with respective osmotic potentials of -0.09, -0.54, or -0.70 MPa using a vapor pressure osmometer (model 5500; Wescor, Logan, Utah). Levels 12 and 20 dS·m⁻¹ were obtained by adding NaCl to the control nutrient solution. These dose levels were selected based on the results of Patil and Patil (1983), where 12 dS·m⁻¹ resulted in a slight reduction in growth and 20 dS·m⁻¹ resulted in a moderate to severe reduction in growth.

Treatments were applied beginning on 16 Nov. 1991, when height of the plants was 623 ± 21 cm (mean ± SE) and diameter of the base of the stems was 12.4 ± 0.3 mm. The NaCl treatments were administered by increasing the EC of solutions 2 dS·m⁻¹ per day to reach 12 dS·m⁻¹ on 21 Nov. or 20 dS·m⁻¹ on 25 Nov. Plants were watered daily with 250 ml of solution per container, which ensured leaching fraction of ≥15% to 20%. Leaching fraction gradually increased over time to ≈50% for the plants receiving 12 or 20 dS·m⁻¹ since gas-exchange, including transpiration, gradually decreased.

The treatments were arranged in a completely randomized design (n = 6). The air mean high and low throughout the study was 33 and 24°C, and the mean high and low relative humidity was 90% and 78%, as determined by a hygrothermograph (WEATHER-tronics model 5020; Qualimetrics, Sacramento, Calif.).

Net CO₂ assimilation (A) was measured at midmorning about every 8 days from 16 Nov. 1991 to 11 Jan. 1992 using a portable photosynthesis system (model 6200; LI-COR, Lincoln, Neb.) with an infrared gas analyzer (model LI-6250; LI-COR) and a 1-liter chamber. Unless otherwise stated, these and all subsequent measurements were made by selecting recently expanded leaves or leaves close to the stem apex after primary growth ceased on the plants receiving NaCl. All gas exchange measurements were made on 10 cm² of exposed leaf area within the chamber. When foliar toxicity symptoms became visible in NaCl-treated plants, only leaves without visual damage were selected for measurements. All measurements were made at an ambient CO₂ of 360 μl·liter⁻¹ under sunny conditions.

The dependence of A on PPF was determined from 31 Dec. (day 45) to 2 Jan. (day 47) using the closed gas-exchange system previously described. All 18 plants were transferred to a laboratory for measurement and analysis as described by Marler et al. (1994). Light was supplied by a 1500-W quartz halogen lamp suspended above a 2.4-cm-thick thermal filtering water bath. The desired PPF was achieved by varying the distance of the cuvette from the lamp and shading with layers of neutral fabric. The conditions were 31 to 34°C and CO₂ at 355 to 366 μl·liter⁻¹ during these measurements. Apparent quantum yield (θ) was calculated using regression analysis as the

Received for publication 27 July 1995. Accepted for publication 14 Nov. 1995. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

slope of the linear portion (irradiance $\leq 165 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) of the light response curves.

Net CO_2 assimilation was measured as a function of external CO_2 concentration as described by Davis et al. (1987). All 18 plants were transferred to a laboratory on 11 Jan. (day 56) for the measurements, during which ambient air ranged from 31 to 34°C. Incident PPF at the cuvette was set at $1035 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and leaves were provided a 15-min equilibration period before measurements. External CO_2 dose levels varied from 100 to $674 \mu\text{l}\cdot\text{liter}^{-1}$.

Dark respiration (R_d) was measured on four plants per NaCl level on 4 Jan. (day 49). Methods and analysis were as described by Marler et al. (1994). External CO_2 was 369 to $379 \mu\text{l}\cdot\text{liter}^{-1}$ and ambient air was 24 to 26°C during these measurements. The procedure for determining the photosynthetic light response curve (including R_d) was repeated on six plants per NaCl level on 15 Jan. (day 60). The conditions during these measurements were 31 to 33°C and CO_2 at 358 to $365 \mu\text{l}\cdot\text{liter}^{-1}$.

Predawn xylem potential (Ψ_x) was measured with a pressure chamber (model 650; PMS Industries, Corvallis, Ore.) on one leaf per plant ($n = 6$) on 12 Jan., 57 days following initiation of treatments. Osmotic potential (Ψ_π) was measured (Wescor model 5500) on the same day using expressed sap after freezing and thawing of leaves as described by Markhart and Lin (1985).

Chlorophyll fluorescence induction was measured with a fluorescence system (model CF-1000; P.K. Morgan Instruments, Andover, Mass.). Measurements were made on 2-h intervals from sunrise to sunset on several days between 13 Jan. (day 58) to 29 Jan. (day 74). Measurements were made at ambient temperature on the adaxial surface of one recently expanded leaf per plant ($n = 6$) following dark acclimation with the system cuvettes for 15 min. PPF of excitation light for fluorescence induction was $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

A sample of leaves was removed from each tree for mineral analysis on 15 Jan. (day 60). Samples consisted of 20 leaves of all ages sampled from all areas of the canopy. Expanding leaves on control plants were not included. Leaf tissue was consolidated into three replications of two trees each. Plant tissue was dried at 60°C, ground to pass through a 60-mesh ($250 \mu\text{m}$) screen, and analyzed according to Wolf (1982).

Foliar mineral content, A , R_d , CO_2 -use efficiency, θ , Ψ_π , Ψ_x , and chlorophyll fluorescence data were subjected to analysis of variance. Significant comparisons were defined by determining the linear and quadratic models with EC as the independent variable.

Results

Increased root-zone NaCl decreased A as a function of time (Fig. 1). The plants subjected to $12 \text{ dS}\cdot\text{m}^{-1}$ responded with a rapid decrease in A , then stabilized with no further reduction after ≈ 2 weeks. In plants subjected to $20 \text{ dS}\cdot\text{m}^{-1}$, A continued to decrease for the duration of the study. Following 56 days of NaCl

stress, A of plants receiving 12 or $20 \text{ dS}\cdot\text{m}^{-1}$ was 72% or 31% of the control plants, respectively (Table 1).

Dependence of A on PPF was linear up to $165 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for all plants (Fig. 2). Net CO_2 assimilation at the upper end of this PPF range was significantly reduced for plants receiving 12 or $20 \text{ dS}\cdot\text{m}^{-1}$ compared with the control plants. As a result, apparent quantum yield (defined as slope) of the plants receiving 12 or $20 \text{ dS}\cdot\text{m}^{-1}$ was 67% and 50% of the control plants, respectively (Table 1). Dependence of A on PPF in the range of 280 to $1610 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ followed a pattern similar to other species (Fig. 3). Substrate NaCl reduced A to the greatest degree, compared with that of control plants, when A was maximum and light saturated. The PPF at which A became saturated, calculated as 95% of the maximum measured value, was $\approx 1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ regardless of the level of root-zone NaCl. Dark respiration was not influenced by changes in substrate NaCl and ranged from 0.76 to $1.64 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The $R_d:A$ ratio was increased by NaCl, ranging from 0.21 for trees receiving $1 \text{ dS}\cdot\text{m}^{-1}$ to 0.56 for trees receiving $20 \text{ dS}\cdot\text{m}^{-1}$.

Other variables were influenced by NaCl in a manner similar to that of A . Net CO_2 assimilation increased linearly with increased

external CO_2 concentration up to $674 \mu\text{l}\cdot\text{liter}^{-1}$ (data not shown). Relative to plants receiving $1 \text{ dS}\cdot\text{m}^{-1}$, CO_2 -use efficiency (defined as slope) was depressed 16% or 36% by 12 or $20 \text{ dS}\cdot\text{m}^{-1}$ (Table 1). Root-zone NaCl reduced Ψ_x of sapodilla leaves more than two-fold when compared to leaves of the control plants (Table 1). Although not to the same degree as Ψ_x , NaCl also reduced Ψ_π (Table 1).

Chlorophyll fluorescence of leaves without toxicity symptoms was not correlated with substrate NaCl. Chlorophyll fluorescence was lowest at midday with variable : maximal chlorophyll fluorescence ($F_v:F_m$) ranging from 0.71 to 0.76. Nocturnal $F_v:F_m$ ranged from 0.80 to 0.82. NaCl did not decrease the diurnal depression of $F_v:F_m$ from leaves of control plants further.

Toxicity symptoms became visible on leaves of some plants receiving 12 or $20 \text{ dS}\cdot\text{m}^{-1}$ solution during week 6 after initiating the treatments. These symptoms consisted of a necrosis that progressed in severity with time of exposure and appeared to have no pattern with respect to location within the canopy of leaves with symptoms. There were no recently expanded leaves on these plants by week 6 since they did not visibly grow after the NaCl treatments were begun. As a result, the varia-

Fig. 1. Net CO_2 assimilation (A) of sapodilla plants relative to that of the control plants grown in sand culture as a function of time. Plants were irrigated with complete nutrient solution ($1 \text{ dS}\cdot\text{m}^{-1}$) or with nutrient solution amended with NaCl to 12 or $20 \text{ dS}\cdot\text{m}^{-1}$. Treatments were begun on 16 Nov. 1991. Vertical bars indicate $\pm\text{SE}$ of the mean, $n = 6$.

Table 1. Net CO_2 assimilation (A), apparent quantum yield (θ), CO_2 -use efficiency, leaf osmotic potential (Ψ_π), and predawn xylem potential (Ψ_x) of sapodilla plants as influenced by root-zone NaCl ($n = 6$). Measurements were made 56 to 60 days after beginning treatments.

Characteristic	Root-zone NaCl ($\text{dS}\cdot\text{m}^{-1}$)			Significance
	1	12	20	
A (CO_2 ; $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	6.5 ± 0.5	4.7 ± 0.5	2.0 ± 0.5	$P \leq 0.01^z$
θ (CO_2 ; $\mu\text{mol}/\mu\text{mol}$ of quanta)	0.024	0.016	0.012	$P \leq 0.01^y$
CO_2 -use efficiency (CO_2 ; $\mu\text{mol}\cdot\mu\text{l}^{-1}$ in air)	0.044	0.037	0.028	$P \leq 0.01^y$
Ψ_x (MPa)	-0.3 ± 0.1	-0.6 ± 0.1	-0.8 ± 0.2	$P \leq 0.01^z$
Ψ_π (MPa)	-2.1 ± 0.1	-3.0 ± 0.2	-3.8 ± 0.2	$P \leq 0.01^z$

^zSignificance of linear model.

^yAnalysis of covariance test for homogeneity of slopes.

Fig. 2. Net CO_2 assimilation (A) of sapodilla plants as a function of root-zone electrical conductivity and photosynthetic photon flux (PPF) from 0 to $165 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Data were obtained on 15 Jan. 1992, 60 days after treatments were initiated. Vertical bars indicate $\pm\text{SE}$ of the mean, $n = 6$. Equations for response curves based on the raw data are as follows: $A = -1.10 + 0.024x$, $r^2 = 0.94$ (1 $\text{dS}\cdot\text{m}^{-1}$); $A = -0.53 + 0.016x$, $r^2 = 0.79$ (12 $\text{dS}\cdot\text{m}^{-1}$); $A = -0.47 + 0.012x$, $r^2 = 0.86$ (20 $\text{dS}\cdot\text{m}^{-1}$).

Fig. 3. Net CO_2 assimilation (A) of sapodilla plants ($n = 6$) as a function of root-zone electrical conductivity and photosynthetic photon flux (PPF) from 280 to $1610 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Data were obtained on 15 Jan. 1992, 60 days after treatments were initiated. Vertical bars indicate $\pm\text{SE}$ of the mean, $n = 6$. Equations for response curves based on the raw data are as follows: $A = 7.61(1 - e^{-0.0027x})$, $r^2 = 0.69$ (1 $\text{dS}\cdot\text{m}^{-1}$); $A = 3.99(1 - e^{-0.0035x})$, $r^2 = 0.37$ (12 $\text{dS}\cdot\text{m}^{-1}$); $A = 3.25(1 - e^{-0.0026x})$, $r^2 = 0.33$ (20 $\text{dS}\cdot\text{m}^{-1}$).

Table 2. Mineral concentrations of sapodilla foliage as influenced by root-zone NaCl 60 days after beginning treatments ($n = 3$).

Mineral	Root-zone NaCl ($\text{dS}\cdot\text{m}^{-1}$)			Significance
	1	12	20	
Na ($\text{g}\cdot\text{kg}^{-1}$)	1.1 ± 0.1	16.1 ± 0.2	19.0 ± 0.2	L**, Q**
Cl ($\text{g}\cdot\text{kg}^{-1}$)	4.9 ± 0.2	23.3 ± 0.3	46.0 ± 0.3	L**, Q**
K ($\text{g}\cdot\text{kg}^{-1}$)	8.5 ± 0.1	4.0 ± 0.2	3.5 ± 0.1	L**, Q**
Ca ($\text{g}\cdot\text{kg}^{-1}$)	11.5 ± 0.2	5.5 ± 0.2	8.0 ± 0.2	Q**
P ($\text{g}\cdot\text{kg}^{-1}$)	1.7 ± 0.1	0.8 ± 0.1	0.8 ± 0.1	L**, Q**
Mn ($\text{mg}\cdot\text{kg}^{-1}$)	9.0 ± 1.0	12.1 ± 1.0	18.1 ± 1.0	L**, Q*
Na : K	0.13 ± 0.01	4.03 ± 0.02	5.43 ± 0.02	L**, Q**
Na + K ($\text{g}\cdot\text{kg}^{-1}$)	9.6 ± 0.2	20.1 ± 0.4	22.5 ± 0.4	L**, Q**

*. **Linear (L) or quadratic (Q) models significant at $P \leq 0.05$ or 0.01, respectively.

tion in leaf age was small compared with the continuously growing control plants. The pattern of necrosis was inconsistent within the laminae. Some sections of the symptomatic leaves remained green with no appearances of toxicity. Chlorophyll fluorescence measurements were made on some of the symptomatic leaves containing green sections that were large enough to be accommodated by the cuvettes of the fluorescence system. Midday $F_v : F_m$ for these leaves was 0.59 ± 0.03 , and recovery during the night was only to 0.67 ± 0.05 .

Substrate NaCl increased Na, Cl, and Mn concentrations in leaf tissue and decreased K, P, and Ca concentrations (Table 2). The increase in Cl concentration per unit increase in solution EC between 1 and 20 $\text{dS}\cdot\text{m}^{-1}$ was more than two times that of Na. Thus, the absolute Cl concentration was much higher than the Na concentration in sapodilla plants exposed to substrate NaCl. However, leaf Na of plants receiving 20 $\text{dS}\cdot\text{m}^{-1}$ was 17 times higher than in the control plants, while leaf Cl was only 9 times higher. Combined concentrations of K and Na doubled from 1 to 12 $\text{dS}\cdot\text{m}^{-1}$, but then only slightly increased to 20 $\text{dS}\cdot\text{m}^{-1}$. Substrate NaCl also increased the ratio of Na to K. There was no consistent influence of NaCl on foliar N, S, Mg, Fe, B, Cu, or Zn (data not shown).

We did not measure growth characteristics due to the short duration of the study and the extremely slow growth habit of this species. However, visible stem and leaf expansion were absent on the plants receiving 12 or 20 $\text{dS}\cdot\text{m}^{-1}$ during the 74 days of the study. In contrast, the plants receiving 1 $\text{dS}\cdot\text{m}^{-1}$ had visibly expanding leaves for the duration of the study.

Discussion

The photosynthetic characteristics of sapodilla leaves reported herein are consistent with other tree fruit species (Flore and Lakso, 1990). Photosynthetic capacity of sapodilla leaves is low but well within the range for woody evergreen species (Korner et al., 1979).

Patil and Patil (1983) reported a salt tolerance threshold for sapodilla at an EC_e of 12 $\text{dS}\cdot\text{m}^{-1}$ based on vegetative growth. Plant responses to salinity cannot be quantified without also quantifying environmental conditions (Maas, 1994). Patil and Patil (1983) did not report variables such as temperature, irradiance, or fertilization regimes, so comparing their results with our results is difficult. In light of these difficulties in interpretation, our data and observations indicate that sapodilla may not be as salt tolerant as reported by Patil and Patil (1983). A large reduction in photosynthetic capacity occurred in all plants exposed to NaCl. Foliage died on some plants receiving 12 $\text{dS}\cdot\text{m}^{-1}$ and on all plants receiving 20 $\text{dS}\cdot\text{m}^{-1}$. We did not measure biomass accumulation, but primary growth visibly ceased on all plants receiving 12 or 20 $\text{dS}\cdot\text{m}^{-1}$.

These physiological responses of sapodilla to root-zone NaCl are consistent with those of other woody perennial glycophyte species.

Salinity reduces A of numerous species, including various tropical fruit crops, such as giant granadilla (*Passiflora quadrangularis* L.) (Zozor and Marler, 1992) and guava (*Psidium guajava* L.) (Walker et al., 1979). Apart from these reports, little has been published concerning the influence of salinity on photosynthesis of tropical fruit species.

The diurnal pattern of chlorophyll fluorescence for sapodilla was similar to that observed in other tropical tree species, although the midday depression of $F_v : F_m$ was not as large as that reported for several other species (Marler, 1994). Root-zone NaCl did not influence this diurnal pattern. Therefore, a NaCl concentration that leads to a substantial reduction in A does not appear to increase sapodilla leaf sensitivity to high irradiance stress. The partial recovery of $F_v : F_m$ during the afternoon and complete recovery following sunset indicate that photoinhibition did not occur during midday. Rather, the reduction in photochemical efficiency, as indicated by reduced $F_v : F_m$, likely was due to increased thermal energy dissipation (Demmig-Adams and Adams, 1992). Moreover, light stress is a consequence of absorbed energy beyond that used in photosynthesis (Demmig-Adams and Adams, 1992), and A of NaCl-stressed sapodilla plants was close to zero. Since the salt-stressed plants were exposed to the same high irradiance as the control plants, an increase in efficiency of thermal energy dissipation may have accounted for the lack of influence on $F_v : F_m$ by NaCl. Alternatively, laminae with some necrosis from toxicity exhibited a lack of recovery of $F_v : F_m$ during the night, indicating photoinhibition may have occurred in these leaves when exposed to midday sun. The results are evidence that thermal energy dissipation remained fully functional for >8 weeks after gas exchange was severely inhibited by NaCl.

Sapodilla plants maintained stable dark respiration throughout the study, while A decreased with time of exposure to NaCl. Typical respiratory loss of C may be as high as half of that fixed in photosynthesis (Amthor, 1989). Consequently, respiration should be recognized as a vital component in understanding the growth responses of plants to salinity stress. The 2.7-fold increase in $R_d : A$ due to exposure to NaCl underscores this importance.

Sapodilla does not appear to be efficient at excluding Na^+ or Cl^- from foliage. However, Na^+ exclusion efficiency has decreased with increased salinity (Jacoby, 1964). Therefore, sapodilla may exclude Na^+ and Cl^- at salt concentrations lower than our selected dose levels. Increased leaf Na^+ and Cl^- concentrations also have been reported for subtropical or tropical crops, such as passion fruit (*Passiflora edulis* Sims forma *flavicarpa* Degener) (Utsunomiya and Shigenaga, 1988),

guava (Makhija et al., 1980), avocado (*Persea americana* Mill.) (Downton, 1978), and citrus (Gallasch and Dalton, 1989; Zekri, 1991) when exposed to increased root-zone salinity.

Selectivity for K^+ transport is important under saline conditions to maintain adequate K^+ nutrition. When the $Na^+ : K^+$ ratio exceeds 1, as in this study, Na^+ may be substituted for K^+ in maintaining proper turgor relations (West, 1986). The $Na^+ : K^+$ ratio also increased with increased salinity in macadamia (*Macadamia integrifolia* Maiden and Betche) (Hue and McCall, 1989) and guava (Makhija et al., 1980). Decreased K^+ uptake with increased root-zone salinity has been noted in other subtropical or tropical fruit crops, such as guava (Makhija et al., 1980) and citrus (Patil and Bhambota, 1980).

The photosynthetic characteristics of sapodilla leaves are similar to those of other woody evergreen species. Moreover, the decrease in A and Ψ_m and the increase of Na^+ and Cl^- leaf concentrations indicate that sapodilla plants respond to an increase of NaCl in the root zone in a manner similar to other woody perennial glycophyte species. The species is not exceptionally tolerant of increased root-zone NaCl relative to other agricultural crops as indicated by our measurements of A, observed toxicity symptoms of the foliage, and cessation of primary stem growth when exposed to NaCl.

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