

NOTE

INFLUENCE OF SALINITY ON CO<sub>2</sub> FLUXES, STOMATAL CONDUCTANCE  
AND SPECIFIC LEAF WEIGHT OF JOJOBA<sup>1</sup>

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ABSTRACT

The effects of salinity on rooted cuttings of Jojoba [*Simmondsia chinensis* (Link) Schnieder] were studied in a sand culture system. The plants were exposed to salinity of -0.2, -0.4, -0.8, and -1.6 MPa in which NaCl + CaCl<sub>2</sub> mixtures were added to a ½ strength Hoagland solution. Measurements were taken 48 hours after the addition of salts and weekly thereafter. Attached branches were used for analysis of CO<sub>2</sub> fluxes with a gas analyzer. Stomatal conductance of attached leaves was also measured after 23 days of exposure to salinity with a diffusive resistance meter. Photosynthesis was reduced at -1.6 MPa. Dark respiration remained unchanged and photorespiration was completely disappeared below -0.2 MPa, after 16 days, and reappeared during the stress release period. The significant decrease in stomatal conductance at -1.6 MPa was partially responsible for photosynthesis reduction. The specific leaf weight measured as mg leaf dry weight per cm<sup>2</sup> leaf area was significantly increased at -1.6 MPa.

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اثرات شوری روی تبا دلات گا زکربنیک، هدا بیت روزنه و وزن ویژه برگ در گیاه هوهو پسا  
یوسف رسول زادگان و ال. هوگان

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## خلاصه

اثرات شوری روی قلمه‌های ریشه‌دارهوهوبا *Simmondsia chinensis* (Link) Schnieder در یک سیستم هیدروپونیک مورد مطالعه قرار گرفت. گیاهان در معرض پتانسیل‌های مختلف شوری (۲/۴-۸/۴-۱/۶-۱/۶-۱/۶) که در آن مخلوطی از کلرورسدیم و کلرورکلسیم به محلول غذایی یک دوغلظت هوگلدن اضافه گردیده بود قرار داده شدند. چهل و هشت ساعت بعد از افزودن نمک به محلول‌ها و بیخوابی گیاهان یک هفته بعد از آن گیاهان برداشت گردیدند. در هر برداشت تبادلات گازی گیاهان توسط دستگاه تجزیه‌کننده گاز اندازه‌گیری شد. هدایت روزنه‌ها نیز ۲۲ روز بعد از قرار گرفتن گیاهان در معرض شوری توسط مقایسه و متسنج روزنه اندازه‌گیری گردید. فتوسنتز در گیاهانی که در معرض ۱/۶-۱/۶ مگاپاسکال شوری قرار گرفته بودند کاهش یافت. تنفس در تارهای تغییرنیافت‌ولی تنفس نوری گیاهان در شوری کمتر از ۲/۵- مگاپاسکال بعد از ۱۶ روزگی از بین رفت. و در طول دوره رفع تنش شوری دوباره ظاهر گردید. کاهش معنی‌دار هدایت روزنه گیاهان در ۱/۶-۱/۶ مگاپاسکال تا حدی موجب کاهش فتوسنتز گردید. وزن ویژه برگ که بر حسب میلی‌گرم وزن خشک برای هر سانتی‌متر مربع مساحت اندازه‌گیری شده بود در گیاهانی که در محلول ۱/۶-۱/۶ مگاپاسکال کاهش یافته بودند بطور معنی‌داری افزایش یافت.

## INTRODUCTION

Jojoba [*Simmondsia chinensis* (Link) Schnieder], a member of Buxaceae family, is a long-lived dioecious, evergreen and sclerophyllous shrub native to the Sonoran desert of Mexico and the United States (11). Jojoba which produces seeds containing 40-60% liquid has received widespread attention as a potential agricultural crop for arid environments (12, 13). Jojoba is true xerophyte, capable of tolerating extremely high temperatures and water stresses (3).

Salinity is known to cause a reduction in photosynthetic activity of plants (9, 10, 15). In jojoba, Benzioni (4), working with CO<sub>2</sub> and detached leaf disks from seedlings grown in sand culture showed that 1000 ppm NaCl (-0.8 MPa) had no appreciable negative effect on photosynthesis. Adams *et al.* (1), exposing jojoba seedlings to various salinity levels, found that CO<sub>2</sub> fixation rate did not change significantly at or below -0.9 MPa of substrate salinity.

The closure of stomata under stress conditions might be partially responsible for reduction in photosynthesis. It has been reported that stomata usually remain fully open until a critical value of leaf water potential is reached (14). However, in some plants stomatal conductance decreases linearly with decreases in xylem pressure potentials (5). In

jojoba, no significant decreases in stomatal conductance was observed at substrate salinity of  $-0.9$  MPa (2).

The present work has been undertaken to explain the possible ways in which jojoba endures the extreme desert conditions and the level of salinity which causes stomatal closure and inhibits its  $\text{CO}_2$  exchange processes. The effect of salt removal on the reversibility of salinity stress on  $\text{CO}_2$  exchange processes was also studied in this work.

## MATERIALS AND METHODS

### Plant Material

To reduce genetic variability which is often caused by use of heterogenous seedlings (2), cuttings from female jojoba plants were used in this study. Sixty well rooted cuttings from each of four clones were transplanted into the containers of the sand culture system. The sand culture system was constructed in an evaporative cooled green-house. During the establishment period (three months), the plants were irrigated with half-strength Hoagland solution, six times daily (3 min every 2 hr from 9 A.M. to 9 P.M.). Distilled water was added to the solution as needed, to make up for evapotranspiration losses. The solution was renewed biweekly and every other day its pH was adjusted within the range of 5.2 -6.5 by the addition of 0.1 N KOH or 0.1 N HCl.

### Treatment Application

For the salinity treatments, mixtures of  $\text{NaCl} + \text{CaCl}_2$  (1:1 molar ratio) at four levels ( $-0.2$ ,  $-0.4$ ,  $-0.8$ , and  $-1.6$  MPa) were used. The base half-strength Hoagland solution ( $-0.04$  MPa) was used as a control. The experiment was designed as a randomized complete block, each block being a different clone. To prevent shock at the time of salt addition, the osmotic potential of the solution was lowered gradually by 0.1 MPa per day before 9 A.M. until the desired salinity level was reached. During the treatment period, plants were

irrigated with the solution for 2 min every hour from 9 A.M. to 9 P.M. so as to prevent excessive drying of the sand and accumulation of salts. During the treatment period, the light intensity inside the green-house varied between 48 and 75 Klx, the relative humidity was held at about 60%, and minimum and maximum temperatures were 17-19°C (night) and 24-30°C (day) respectively. Twenty four days after the last addition of the salts, the solution for all the treatments was changed to the control level in order to study the reversibility of the salinity effects on jojoba (stress release period).

#### Data Recording

First data recording was made 48 hr after the last increment of the salt was added and weekly thereafter for five weeks. Physiological measurements were confined to the first three-four fully expanded leaf pairs which were formed during or after establishment period.

CO<sub>2</sub> Fluxes. CO<sub>2</sub> fluxes were determined using a closed system with a Beckman model 865 infra-red gas analyzer as described by Delany (8). Prior to measuring CO<sub>2</sub> fluxes, plants were placed under a bank of seven Sylvania 500 Watt flood lamps (54.9 Klx), for 30 min to allow stomata to open fully. Attached branches with four-five mature leaves, produced during the treatment period, were sealed in a 250 ml Plexi-glass chamber under the lamps. The temperature inside the chamber was 24±1 C and the air in the chamber circulated at the rate of 1.75 l/min. Net photosynthesis ( $P_n$ ), dark respiration (DR), and photorespiration (PR) were calculated from the recorder tracing of the gas analyzer.

Stomatal conductance. Stomatal conductance ( $g_s$ ) of adaxial leaf surfaces were measured with a diffusive resistance meter, using the procedures provided by Kanemasu *et al.* (16). Six leaves, each one at the fourth node from the growing point were used for these measurements. The stomatal conductance measurements were made in the green-house and only

after 23 days of exposure to salinity.

Specific leaf weight. Specific leaf weight (SLW), was determined as mg leaf dry weight per cm<sup>2</sup> leaf area. Leaf area was measured with an automatic area meter (Model AAM-5 Hayashi Denko Co. Tokyo, Japan), after being detached and then the leaves were oven dried at 80°C for dry weight determinations.

The statistical design employed was randomized complete block with four blocks (replications). Each measurement was taken twice on each of two separate plants per pot and were averaged. Duncan's multiple range test was used for comparison of means.

## RESULTS AND DISCUSSION

### CO<sub>2</sub> Fluxes

Net photosynthesis ( $p_n$ ) was significantly ( $P < 0.05$ ) reduced at -1.6 MPa on day 16 (Table 1). Upon transferring plants to the control solution,  $p_n$  at -1.6 MPa returned to the original level again. This might be an indication of jojoba's photosynthesis system adjusted to salinity. Similar data have been reported by Adams *et al.* (1) who found no significant decrease in CO<sub>2</sub> fixation rate above -0.9 MPa of NaCl+CaCl<sub>2</sub> salinity.

Dark respiration was not influenced by any of the salinity levels during the course of this study. However, reduced DR under severe stress conditions in the field has been reported for jojoba (3).

Photorespiration in jojoba was severely affected below -0.2 MPa after 16 days (Table 1). Photorespiration which was estimated by subtracting DR from post-illumination burst (PIB) of CO<sub>2</sub> released, was not detectable due to apparent loss of PIB. The disappearance of PR was initially attributed to the higher flow rate of air passing over the plant. However, with a further reduction of flow rate no PIB was evident.

Table 1. Influence of NaCl+CaCl<sub>2</sub> salinity levels and treatment periods on CO<sub>2</sub> exchange parameters of jojoba under sand culture system.

Days after	Salinity level (MPa)	CO <sub>2</sub> exchange parameters					Stomatal Conductance cm sec <sup>-1</sup>	Specific leaf weight mgdwt cm <sup>-2</sup>
		Net photosynthesis mg CO <sub>2</sub> dm <sup>-2</sup> h <sup>-1</sup>	Dark respiration mg CO <sub>2</sub> dm <sup>-2</sup> h <sup>-1</sup>	Photorespiration mg CO <sub>2</sub> dm <sup>-2</sup> h <sup>-1</sup>				
2	0	6.99 a	2.46 a	2.26 a	-	-	14.28 a	
	0.2	7.56 a	2.27 a	3.00 a	-	-	14.57 a	
	0.4	6.02 a	2.37 a	3.02 a	-	-	14.39 a	
	0.8	7.79 a	2.05 a	3.28 a	-	-	14.46 a	
	1.6	4.74 a	2.65 a	2.20 a	-	-	17.14 a	
9	0	7.58 a	2.16 a	1.60 a	-	-	14.06 a	
	0.2	7.33 a	2.68 a	1.54 a	-	-	14.61 a	
	0.4	7.39 a	1.81 a	1.83 a	-	-	14.53 a	
	0.8	7.46 a	2.14 a	1.53 a	-	-	14.13 a	
	1.6	5.10 a	2.55 a	1.40 a	-	-	19.04 b	
16	0	7.54 a	1.84 a	1.99 a	-	-	14.02 a	
	0.2	8.31 a	1.70 a	0.24 a	-	-	16.54 ab	
	0.4	7.85 a	1.71 a	? <sup>f</sup>	-	-	15.23 a	
	0.8	5.58 ab	2.09 a	? <sup>f</sup>	-	-	16.70 ab	
	1.6	4.52 b	2.05 a	? <sup>f</sup>	-	-	19.96 b	
23	0	6.12 a	1.81 a	1.43 a	-	-	14.85 a	
	0.2	6.06 ab	1.84 a	0.26 a	-	-	14.70 a	
	0.4	6.52 a	1.93 a	? <sup>f</sup>	-	-	15.49 a	
	0.8	5.94 ab	1.75 a	? <sup>f</sup>	-	-	18.33 ab	
	1.6	3.41 b	2.94 a	? <sup>f</sup>	-	-	20.30 b	
30†	0	6.13 a	2.31 a	1.03 a	-	-	14.13 a	
	0.2	6.28 a	2.37 a	0.37 a	-	-	14.37 a	
	0.4	5.79 a	2.50 a	0.22 a	-	-	14.82 a	
	0.8	4.89 a	2.34 a	0.14 a	-	-	16.31 ab	
	1.6	6.34 a	2.46 a	0.03 a	-	-	18.49 b	
37†	0	6.91 a	2.31 a	1.59 a	-	-	14.83 a	
	0.2	7.94 a	2.85 a	0.86 a	-	-	14.11 a	
	0.4	6.53 a	2.65 a	0.28 a	-	-	14.07 a	
	0.8	6.43 a	2.65 a	1.19 a	-	-	14.91 a	
	1.6	8.22 a	2.13 a	1.79 a	-	-	16.39 a	

† - Cuttings were no longer in saline solution. Starting on day 24, the salinity level of all cuttings was returned to control level (0.04 MPa)  
 ‡ - Within columns and at a given date, means associated with the same lower case letter are not significantly different at 5% level according to Duncan's multiple range test.  
 § - not detectable  
 ¶ - Dashes indicate that measurements were not taken.

The loss of PR might be related to the reduced level of substrate available for glycolate production and its conversion to serine. Photorespiration was recovered upon transferring the plants to control solution, which confirms the above statement. Photorespiration is regarded as a wasteful process in  $C_3$  plants, accounting for the oxidation of as much as 50% of the carbon fixed in photosynthesis (19). Reduced PR probably improves carbon balance of stressed plants. Further investigation is needed to verify this possibility.

#### Stomatal Conductance

Stomatal conductance ( $g_s$ ) on day 23 was significantly ( $P < 0.05$ ) reduced at  $-1.6$  MPa (Table 1). The leaf water potential against stomatal conductance indicated that complete stomatal closure occurred at leaf water potentials equal to  $-3.2$  MPa (Fig. 1). These data like those of Adams *et al.* (1, 2) indicate that stomata are not completely closed at  $-1.6$  MPa.

#### Specific Leaf Weight

Specific leaf weight (SLW) has been used to estimate the photosynthetic activity of crop plants because in some cases it increases with the increase of photosynthesis (6, 7, 17). However, in our experiment, SLW increased at  $-1.6$  MPa while  $P_n$  was reduced. This was attributed to the increased leaf thickness in response to salinity. The following relationships were found between leaf thickness in mm (data not presented), SLW, and solution osmotic potentials:

$$\text{Leaf thickness} = 0.64 + 0.11 (\psi \text{ root media}), r = 0.83^*$$

$$\text{SLW} = 14.37 + 3.4 (\text{leaf thickness}), r = 0.91^*$$

Furthermore, the percent reduction in leaf area expansion at  $-1.6$  MPa was greater than percent reduction in net photosynthesis (70% and 45% respectively) which might explain the apparent paradox.

The loss of PR might be related to the reduced level of substrate available for glycolate production and its conversion to serine. Photorespiration was recovered upon transferring the plants to water solution, which eliminated the above statement. The carbon fixed in photosynthesis (19) improves carbon balance of stressed plants. Investigation is needed to verify this possibility.

Stomatal conductance ( $g_s$ ) on day 13 was significantly ( $P < 0.05$ ) reduced at -1.6 MPa (Table 1). The stomatal closure against a water potential equal to -1.6 MPa (Fig. 1) indicated that the stomata were not completely closed at -1.6 MPa.

Specific leaf weight (SLW) has been used to estimate the photosynthetic activity of crop plants because in some cases it increases with the increase of photosynthesis (7, 11). However, in our experiment, SLW increased at -1.6 MPa while  $P_n$  was reduced. This was attributed to the increase in leaf thickness in response to the water stress.

There were no significant relationships between leaf thickness in mm (data not presented), SLW, and solution osmotic potential.

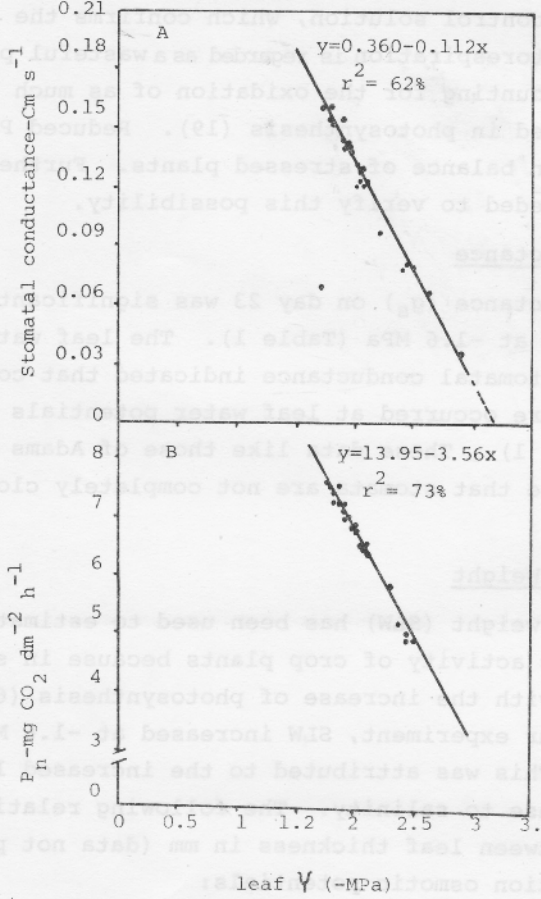


Fig. 1. Stomatal conductance (A) and net photosynthesis (B) of jojoba leaves in relation with leaf xylem water potentials.

Furthermore, the percent reduction in leaf area expansion at -1.6 MPa was greater than percent reduction in net photosynthesis (70% and 42% respectively) which might explain the apparent paradox.



It seems that the ability of jojoba plants to maintain a positive net photosynthesis by reduction of PR under severe stress conditions, the incomplete closure of stomata, and the ability of its photosynthesis system to function at relatively high salt concentrations may contribute to its survival in the desert conditions.

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