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Salinity effects on growth, leaf-ion content and seed production of Lesquerella fendleri (Gray) S. Wats

Catherine M. Grieve *, James A. Poss, Terence J. Donovan, Leland E. Francois

US Salinity Laboratory, 450 W. Big Springs Road, Riverside, CA 92 507, USA

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Abstract

Little information is available on the response of lesquerella grown under saline conditions. This field study was initiated to determine the responses of lesquerella to salinity relative to growth, seed yield and oil content. Six salinity treatments were imposed on a Holtville silty clay (clayey over loamy, montmorillonitic (calcareous), hyperthermic Typic Torrifluvent). The plots were irrigated with Colorado River water artificially salinized with NaCl and CaCl₂ (1:1 by weight). Electrical conductivities of the irrigation treatments in both years were 1.4, 2.2, 4.0, 6.0, 8.0, and 10.0 dS m⁻¹. Vegetative growth, leaf-ion content, seed yield, oil content and fatty acid composition of the seed were measured. Seed yield decreased from 2100 kg ha⁻¹ under nonsaline control conditions to 650 kg ha⁻¹ at the highest salinity level. Analysis of the combined two-year data showed a 19% reduction in seed yield for each unit increase in soil salinity above a threshold of 6.1 dS m⁻¹. Based on these results, lesquerella can be classified as a salt tolerant crop. In response to increases in salinity, leaf Ca and Cl increased, whereas Mg decreased. Sodium was effectively excluded from leaf tissue at all levels of salinity. Concentrations of Na were generally an order of magnitude lower in lesquerella leaves than has been reported in leaves of other cruciferous crops grown under saline field conditions. Total oil content of the seeds increased slightly, but significantly, with increases in soil salinity. The fatty acid composition showed a minor, but again significant, increase in linolenic acid (C18:3) content as salinity increased. With this exception, oil composition did not change with salinity level, including the content of lesquerolic acid in the oil. © 1997 Elsevier Science B.V.

Keywords: Hydroxy fatty acids; Leaf ion content; Lesquerolic acid; Salinity; Seed oil; Sodium exclusion

1. Introduction

* Corresponding author. Fax: +1 909 3424962; e-mail: cgrieve@ussl.ars.usda.gov

Lesquerella fendleri, a species native to the arid and semiarid regions of southwestern US, has been proposed as an important industrial seed oil

0926-6690/97/\$17.00 © 1997 Elsevier Science B.V. All rights reserved. PII \$0926-6690(97)00076-9 crop (Thompson and Dierig, 1988). Research in Arizona demonstrated that the crop is adaptable to production under intensive field cultivation and various management strategies for optimizing seed yield and oil content have been reported. While intensive germplasm selection and breeding trials have resulted in seed yields in excess of 1800 kg ha⁻¹, yields are strongly dependent on planting and harvesting dates, method of harvesting, plant population, nitrogen status and irrigation timing (Dierig et al., 1993; Coates, 1994, 1996; Brahim et al., 1996; Nelson et al., 1996).

Lesquerella seeds contain 19-30% oil. The major constituent is lesquerolic acid, a hydroxy fatty acid, which has great potential for use in the production of lubricants, plastics, surfactants, pharmaceuticals, and cosmetics (Carlson et al., 1990; Kleiman, 1990). For many oil seed crops, variable environmental conditions may produce wide differences in oil quantity and composition (Knowles, 1972; Shafii et al., 1992). In response to salinity, the oil content of safflower (Carthamus tinctorius L.) decreased, whereas its composition was unaffected (Yermanos et al., 1964; Irving et al., 1988). However, both oil content and composition of a high-oleate safflower were changed by salt stress, resulting in higher linoleate values with increasing salinity (Irving et al., 1988). Salinity had no effect on either oil percentage or fatty acid composition of canola (Brassica napus L.) (Francois, 1994) or sunflower (Helianthus annuus L.) (Francois, 1996). Crambe (Crambe abyssinica Hochst. ex. R.E. Fries) seed oil content and its erucic acid level were unchanged by salinity. However, with increases in salinity, the percentages of oleic and eicosenoic acids increased, whereas linolenic acid tended to decrease (Francois and Kleiman, 1990).

Based on its natural geographic distribution in arid regions, it is likely that lesquerella has developed adaptive mechanisms for coping with drought, salinity stress and/or other environmental challenges. Continued agronomic development of lesquerella may be extended to areas where salinity or sodicity problems may already exist or may develop. A two-year study was initiated to determine the effect of salinity on the growth, seed yield and oil content of lesquerella.

2. Materials and methods

This study was conducted at the Irrigated Desert Research Station, Brawley, CA, on a Holtville silty clay soil. The crop was grown in 6.0×6.0 m plots enclosed by acrylic-fortified fiberglass borders that extended 0.75 m into the soil. The tops of the fiberglass borders protruded 0.15 m above the soil level of the plot and were covered with a berm 0.18 m high and 0.60 m wide. Walkways, 1.2 m wide between plots, and good vertical drainage effectively isolated each plot.

Prior to planting, triple superphosphate was mixed into the top 0.25 m of soil at the rate of 73 kg P⁻¹ ha⁻¹. To assure adequate N fertility throughout the experiment, $Ca(NO_3)_2$ was added at the rate of 0.14 kg N ha⁻¹ mm⁻¹ of water applied at every irrigation. Because the soil contained adequate levels of K, no additional K was added.

On 19 October 1993 and 7 October 1994, lesquerella seeds, obtained from Dr A.E. Thompson, US Water Conservation Laboratory, Phoenix, AZ, were sown by broadcasting in level plots at the rate of 10 kg ha⁻¹. Stand establishment in 1993 was less than optimum in a few plots and these were reseeded on 5–9 November 1993.

The experimental design consisted of six salinity treatments replicated three times in a randomized block design. At the time of planting, the soil profiles were still salinized from a previous experiment. To assure good germination, 75 mm of nonsaline water (1.4 dS m⁻¹) was applied to each plot prior to planting to leach salts from the top 0.15 m of soil.

The crop was irrigated with nonsaline irrigation water for ≈ 12 weeks after planting. In the first year, 155 mm water was applied during this period, 125 mm was applied during the corresponding period in the second season. In both experimental years, differential salinization was initiated on 18 January when plant heights ranged from 6 to 10 cm. To avoid the effects of salt shock, the salinity in the irrigation water was increased in two steps over a three-week period with the first irrigation applied at one-third strength salinity, the second irrigation at two-

Table 1 Average electrical conductivities of saturated-soil extracts (EC_e) measured at three depths for six salinity treatments for 2 years

Soil sample depth (m)	Electrical conductivity (dS m ⁻¹)								
	1.4	2.2	4.0	6.0	8.0	10.0			
	1993-1994								
0-0.3	2.6 ± 0.2^{a}	3.5 ± 0.3	4.9 ± 0.5	5.8 ± 0.6	6.2 ± 0.4	7.8 ± 0.5			
0.3-0.6	4.9 ± 0.4	7.3 ± 0.4	8.0 ± 0.5	9.3 ± 0.8	7.8 ± 0.7	9.5 ± 0.6			
0.6-0.9	6.1 ± 0.6	8.4 ± 0.8	7.3 ± 1.1	8.8 ± 0.4	8.3 ± 0.7	10.2 ± 0.9			
Avg.	4.6 ± 0.4	6.4 ± 0.6	6.7 ± 0.5	8.0 ± 0.5	7.4 ± 0.4	9.2 ± 0.6			
	1994-1995								
0-0.3	3.1 ± 0.4	3.4 ± 0.2	5.7 ± 0.4	6.9 ± 0.4	7.7 ± 0.3	9.2 ± 0.5			
0.3-0.6	6.5 ± 0.6	7.8 ± 0.4	8.7 ± 0.8	10.4 ± 0.6	11.0 ± 0.7	11.1 ± 0.8			
0.6-0.9	7.5 ± 1.0	9.0 ± 0.6	9.5 ± 1.1	9.2 ± 0.4	10.0 ± 0.8	11.0 ± 0.6			
Avg.	5.7 ± 0.5	6.8 ± 0.5	7.9 ± 0.6	8.8 ± 0.4	9.9 ± 0.5	10.4 ± 0.4			

^a Means ± SE of three samples.

thirds salinity and all subsequent irrigations at full strength salinity. The salinization of the irrigation water was accomplished by adding equal weights of NaCl and CaCl2 to Colorado River water until the desired salt concentrations were achieved. In both study years, the electrical conductivities of the six irrigation waters (EC_{iw}) were 1.4 (the control: Colorado River water), 2.2, 4.0, 6.0, 8.0 and 10.0 dS m⁻¹. All plots were irrigated about every 2 weeks throughout the study to keep the soil matric potential of the control treatments above -85 J kg^{-1} in the 0.15-0.3 m zone. For the first year of the experiment, final irrigations were on: 12 April 1994 (treatments 5 and 6), 26 April 1994 (treatments 3 and 4) and 11 May 1994 (treatments 1 and 2). The final irrigations of the same treatments for the second year took place on 1, 15 and 29 May 1995. The total irrigation water applied after planting for both years was 455 mm. Total rainfall was 40 mm in the first cropping season and 74 mm in the second season.

Soil samples were collected from each plot prior to planting and again 5 and 14 weeks after salinization. Three soil cores per plot were taken in 0.3 m increments to a depth of 0.9 m. In both years, electrical conductivities of the saturated-soil extracts (EC_e) were averaged for each of the three depths for both years (Table 1).

The mean high temperature from planting to initial flowering was 25.6°C for 1993–1994 and 23.2°C for 1994–1995. Low night temperatures for the same periods were 7.2 and 7.9°C, respectively. During flowering, the mean high temperature was 24.7°C in 1994 and 24.1°C in 1995. The duration from flowering to seed maturation depended upon the degree of salinity stress the plants encountered. For plants in the plots irrigated with the most saline water, this period was 85 d, during which the mean high and low temperatures were 30.7 and 10.4°C in 1994 and 30.7 and 12.6°C in 1995, respectively.

On 15 March 1995, mature fully expanded leaves were sampled for mineral analysis. Blades were washed with deionized water, dried at 70°C and finely ground in a blender. Calcium, magnesium, sodium, potassium and phosphate were determined on nitric-perchloric acid digests of the plant material by inductively coupled plasma optical emission spectrometry. Chloride was determined on nitric-acetic acid extracts by coulometric-amperometric titration.

For both years, five plants were randomly selected from each plot at the time of harvest and the height measured from the soil surface to the terminal growth.

Harvest began on 13 June 1994 and on 3 July 1995 and in both years, extended over a three-

Table 2 Yield, seed index, plant population and plant height of lesquerella grown at six salinity levels

Irrigation water salinity (dS m ⁻¹)	Yield kg ha ⁻¹	1000-seed weight (g)	Plant population (plants/ha)	Plant height (m)	
1993–1994			——————————————————————————————————————		
1.4	2192a	0.644	900 000	0.469	
2.2	2016	0.636	910 000	0.46	
4.0	1458	0.684	990 000	0.451	
6.0	1479	0.652	960 000	0.386	
8.0	1090	0.620	960 000	0.381	
10.0	671	0.612	1 030 000	0.331	
LSD (0.05)	781	0.012	NS	0.031	
$P > F^b$	0.0107	0.0509	0.4465	0.0001	
19941995					
1.2	2034	c	1 200 000	0.497	
2.2	2068	_	1 140 000	0.494	
4.0	1336	-	1 300 000	0.439	
6.0	1105	_	1 300 000	0.418	
8.0	809	_	1 400 000	0.363	
10.0	606	-	1 250 000	0.339	
LSD (0.05)	400		NS	0.023	
$P > F^{b}$	0.0001		0.3201	0.0001	

NS, not significant.

week period. The later harvest day in 1995 corresponded to the later planting period. Plants subjected to the most severe salinity stress matured substantially earlier than those grown under nonsaline conditions. Thus, total time from sowing to harvest ranged from 240 to 260 d. To determine seed yield, a 1.86 m² area was hand-harvested from the center of each plot. Plants were air-dried for 2 weeks. Capsules were threshed and the seed cleaned, then weighed. In 1993–1994 trial only, additional plants per plot were harvested. The capsule-bearing area of each plant was divided horizontally into three sections to determine the effect of salinity on the physiological age of the seed. The seeds from each section were threshed, cleaned and weighed. The weight per 1000 seeds was recorded.

Seed oil composition and quantity of the 1993–1994 crop were determined by Bliss Phillips, USDA-ARS, National Center for Agricultural Utilization Research, Peoria, Il. Detailed descriptions of the analytical procedures are given in Dierig et al., 1996.

3. Results and discussion

Lesquerella plant populations in the experimental plots ranged from about 900 000 to 1 000 000 plants ha -1 in the 1993-1994 cropping season and from about 1 100 000 to 1 400 000 plants ha $^{-1}$ the second season. The populations for both years were not significantly influenced by salinity (Table 2). Mean seed yield of hand-harvested plants irrigated with waters at 1.4 and 2.2 dS m⁻¹ exceeded 2000 kg ha⁻¹ in both years (Table 2). Yield decreased consistently and significantly as salinity increased. Although the weight of 1000 seeds (determined in the 1993-1994 trial only) varied significantly from 0.684 to 0.612 g, the reduction in total yield was attributed primarily to a decrease in total seed numbers. Reduction in seed number was undoubtedly associated with salt-induced decreases in plant size, as exemplified by the significant decreases in plant height (Table 2). At the lower levels of salinity, plant heights were similar to those reported by Coates (1996).

^a Values are the means of three replications.

^b Probability that a significant F value would occur by chance.

^c Not determined.

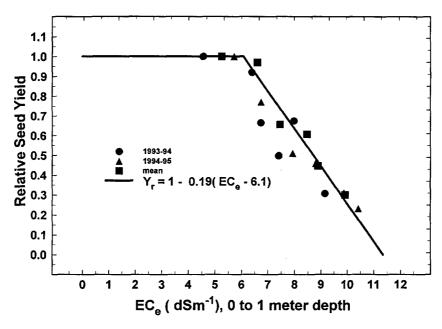


Fig. 1. Relative seed yield of lesquerella as a function of increasing soil salinity.

The combined seed yield data for both years were statistically analyzed with a linear response model (van Genuchten and Hoffman, 1984). The results indicate that the threshold (i.e., the maximum allowable EC_e without a yield decline) for lesquerella was 6.1 dS m⁻¹ (Fig. 1). Each unit increase in salinity above the threshold reduced yield 19%. Relative yield, Y_r , for any EC_e exceeding the threshold can be calculated with the equation presented in Fig. 1. According to the Maas and Hoffman (1977) salt tolerance classification system, lesquerella can be rated as tolerant to salinity. Although the species exhibited a threshold in excess of 6 dS m⁻¹, the rate of yield decline above the threshold was much greater than for most other crops in the tolerant category (Maas, 1990). The salt tolerance of lesquerella is 'intermediate' in comparison with two other oil seed crops in the plant family Brassicaceae. Crambe has been classified as moderately sensitive, with a tolerance threshold of 2.0 dS m⁻¹ and a slope of 6.5% per dS m⁻¹ (Francois and Kleiman, 1990). At the other extreme, canola has been rated as salt tolerant. Depending on the cultivar, the threshold for canola is 10-11 dS m⁻¹ and the slope is 13-14% per dS m⁻¹ (François, 1994).

Seed moisture was 2.5% at the time of oil analysis and was unaffected by treatment (data not presented). Seeds contained about 24% oil and slight, but statistically significant, differences in total oil content occurred in response to salinity (Table 3). Salt treatment had no effect on the concentrations of palmitic (C16:0), palmitoleic (C16:1), stearic (C18:0), oleic (C18:1), linoleic (C18:2), lesquerolic (C20:1-OH) and auricolic (C20:2-OH) fatty acids. However, the content of linolenic acid (C18:3) decreased from 14.1 to 12.9% as salinity increased. Lesquerolic acid comprised more than half (54-56%) of the total seed oil. The fatty acid profile presented in Table 3 is very similar to that obtained for plants grown under optimum field conditions and harvested 264 d after sowing (Brahim et al., 1996).

In response to increased salinity, concentrations of calcium in lesquerella leaves significantly increased, whereas magnesium decreased (Table 4). As salinity and rootzone-calcium increased, the Ca/Mg ratio in the leaves rose from 3 to 9. Calcium is strongly competitive with Mg and the binding sites on the root plasma membrane ap-

Table 3
Oil content and fatty acid composition of lesquerella seed grown at six salinity levels in 1993–1994

Irrigation water salinity (dS m ⁻¹)	Oil%	C16:0%	C16:1%	C18:0%	C18:1%	C18:2%	C18:3%	C20:10H%	C20:20H%
1.4	23.7ª	1.4	0.7	1.7	15.6	7.0	14.1	54.2	4.0
2.2	24.4	1.4	0.7	1.7	15.4	7.4	13.7	54.5	3.7
4.0	24.8	1.3	0.7	1.7	15.3	7.2	13.8	54.6	4.0
6.0	24.6	1.3	0.6	1.6	15.5	7.1	13.7	54.8	3.9
8.0	24.8	1.3	0.7	1.6	14.9	7.2	13.4	55.6	3.8
10.0	24.3	1.4	0.7	1.6	15.2	7.7	12.9	55.4	3.5
LSD (0.05)	0.9	NS	NS	. NS	NS	NS	0.9	NS	NS
$P > F^b$	0.0111	0.6605	0.6560	0.9748	0.8727	0.2818	0.0155	0.7807	0.6719

NS, Not significant.

pear to have less affinity for Mg than Ca. High concentrations of substrate Ca frequently lead to marked reductions in leaf-Mg which, in turn, have been associated with declines in photosynthetic rate, water use efficiency and plant growth (Grattan and Grieve, 1994). Leaf Cl also significantly increased as salinity levels increased. Although no injury was noted, lesquerella growth may have been limited by Cl content in leaf tissue. Certain plants are intolerant of high external Cl, due to excessive accumulation of Cl in plant tissue or to Cl-induced nutritional imbalances, such as inhibition of phosphate or nitrogen uptake and metabolism. Although phosphate concentrations tended to decrease with increasing salinity, this trend was not significant. Leaf N was not determined in this study. As substrate Na increased, lesquerella appeared to possess an effective mechanism for restricting the accumulation of Na by the leaves when grown at moderate or high salinities. Ion distribution in other lesquerella organs was not determined in this study and it is possible that Na may have accumulated in and been confined to stem or root tissue. Other regulatory mechanisms may also operate to limit accumulation of a potentially toxic ion such as Na, in lesquerella leaves. In contrast, many other cruciferous seed oil crops appear to lack a comparable ability for Na exclusion. Canola and crambe, for example, were Na accumulators when grown in field trials conducted at the same site as this experiment. In response to soil salinity of about 10 dS m^{-1} , canola leaves accumulated over 800mmol Na kg⁻¹ dry weight (Francois, 1994), whereas Na levels in crambe leaves grown in soils salinized at 6 dS m⁻¹ were around 600 mmol kg⁻¹ dry weight (Francois and Kleiman, 1990). In lesquerella leaves, K accumulation was greater than Na, in contrast to the concentration of these ions in the substrate. Maintenance of adequate Kstatus is essential for normal cell functions and under saline conditions, the K/Na balance in the plant becomes critical to plant performance. The K levels in lesquerella leaves were not significantly affected by salinity treatment in sharp contrast to other Brassicaceae. As a result, the K/Na ratios in lesquerella leaves were at least an order of magnitude higher than those reported in salt-stressed crambe, canola, and numerous other brassicas (Ashraf and McNeilly, 1990; Francois and Kleiman, 1990; He and Cramer, 1992; Francois, 1994).

The response of plants to salinity depends not only on the total electrolyte concentration in the rootzone, but also on the ionic composition of the salts contributing to salinity. Lesquerella, subjected to chloride-salinity containing ≈ 1:1 Na and Ca concentrations (equivalent basis), exhibited several unique responses that point to further avenues of research. The sodium exclusion response, as well as the ability to regulate potassium uptake from high sodium substrates, exhibited by salt-stressed lesquerella suggests that the crop may be well adapted to growth in sodic soils. Con-

^a Values are the means of three replications.

^b Probability that a significant F value would occur by chance.

Table 4
Mineral composition of lesquerella leaves grown at six salinity levels in 1994–1995

Irrigation water salinity (dS m ⁻¹)	Mineral composition (mmol kg ⁻¹ dry weight)							
	Ca	Mg	Na	K	P	Cl		
1.4	1816ª	557	17.3	384	77.4	689		
2.2	1920	683	10.7	383	60.9	950		
4.0	2125	481	30.9	379	63.1	1277		
6.0	2102	321	18.0	388	66.1	1608		
8.0	2152	286	47.6	435	57.3	1945		
10.0	2230	257	11.9	391	52.0	1999		
LSD (0.05)	160	96	NS	NS	NS	460		
$P > F^{\mathrm{b}}$	0.0004	0.0001	0.2565	0.9506	0.2959	0.0002		

NS, Not significant.

versely, lesquerella accumulates high concentrations of Ca and Cl in its leaves. Either or both of these ions may contribute to the reduction in plant growth and yield. Together, these findings (possible sensitivity to Ca and Cl and apparent exclusion of Na) from the present field trial suggest that the crop might be suitable for production on sodic soils or in areas where the available irrigation waters are sodium-dominated and are high in sulfate, rather than in chloride, salts. The response of lesquerella to sulfate-salinity should be studied to determine if the crop could fill a niche in drainage water reuse systems (Rhoades, 1989) where only moderate tolerance is required and where its unique ion uptake responses could be exploited.

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^a Values are the means of three replications.

^b Probability that a significant F value would occur by chance.

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