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Temperature and elevation effects on plant growth, development, and seed production of two *Lesquerella* species

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Abstract

A potential new alternative oilseed crop from the genus *Lesquerella* is being domesticated for the southwestern United States and other arid climates of the world. This crop has seed oil rich in hydroxy fatty acids used to produce a variety of industrial, cosmetic, and pharmaceutical products. Many of the industrial products are replacements for non-degradable and non-renewable petroleum-based products such as hydraulic fluids, surfactants, 2-cycle engine oils, automotive oils, protective coatings, drying agents, and plastics. *L. fendleri* is the main species being utilized for crop development, although other species are being utilized for introgression of useful traits into *L. fendleri*. The objective was to determine field sites suitable for crop production. Two species, *L. fendleri* and another we refer to as '*L. pallida* aff.' because it differed from typical *L. pallida* plants in chromosome number and in oil quality, were planted in the fall of 2003 at various sites in Arizona that ranged in elevation from 300 to 1200 m asl, and −13.2 to 38.8 °C in temperature over the growing season. The four sites included Phoenix, Tucson, Safford, and Patagonia. Plants of *L. fendleri* developed flowers and fruits by the week of 21 March at Phoenix and Tucson, but one month later at the two higher elevation sites. Plant height, width, and biomass measured during the season indicated that plants at the two lower elevations grew nearly two times taller and wider, and over five times the biomass of the plants at the higher elevations. Seed yields followed the same trend. However, oil contents were very similar over the four elevations. Plants of *L. pallida* aff. were almost all flowering and fruiting by 04 April at Tucson, two weeks later at Phoenix, and not until 02 May at the two higher elevations. Plants were tallest and widest throughout the season at Tucson until final harvest. Plants at Patagonia at final harvest were as tall and wide, had greater biomass and seed yields than Tucson and Phoenix. These results indicate that *L. fendleri* is suitable for production in areas below 700 m. Plants of *L. pallida* aff. were more productive at the highest elevation of 1219 m. It was not entirely clear as to how plants of either species would have performed at the 884 m elevation site due to high plant mortality at the early growth stage. Results indicate that production areas for *L. fendleri* may be expanded with the introgression of genes from *L. pallida* aff.

Keywords: Biomass production; Elevation gradient; Phenology; Seed yield; Seed oil; New crops

1. Introduction

Lesquerella (Brassicaceae) is a genus with 95–100 species, mostly originating from the United States and Mexico. *L. fendleri* (Gray) Wats. is currently undergoing domestication as a potential alternative industrial oilseed

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crop (Dierig et al., 1993, 2004). *L. fendleri* is found in the wild primarily in eastern Arizona, New Mexico, Texas, and northern Mexico (Dierig et al., 1996; Salywon et al., 2005). Some populations have been identified in the southeastern corner of Colorado and a few in the southeastern corner of Utah (Rollins and Shaw, 1973). This species extends over a wide geographic range of soil types, temperatures, and elevations. The localities range in elevation from sea level to 2500 m. There are distinct ecotypes found at some of these different elevations (Salywon et al., 2005).

Hydroxy fatty acids (HFAs) in the seed oil are characteristic of this genus and of *Physaria*, a closely related genus. These HFAs are similar to those found in castor oil (*Ricinus communis* L.). Castor produces ricinoleic acid (12-hydroxyoctadeca-9-enoic acid, or C18:1-OH) and *Lesquerella* species from the western U.S. and *Physaria* species produce lesquerolic acid (14-hydroxyeicosa-11-enoic, or C20:1-OH) as the primary fatty acid of the seed oil composition (Hayes et al., 1995). These HFAs serve as chemical feedstocks in the production of a variety of products including non-petroleum-based industrial lubricants such as greases, hydraulic fluids, and motor oils (Roetheli et al., 1991; Dierig et al., 2004). Personal care products and pharmaceuticals also contain HFAs. The southwestern U.S. is the targeted region of production for *L. fendleri*, which is grown as a winter annual with an expected requirement of at least 142,000 ha based on current usage of castor oil.

Other species have desirable traits to offer in the breeding improvement of *L. fendleri*. Some have significantly higher amounts of HFA in their seed oils than *L. fendleri*. *Lesquerella pallida* (Torr. & Gray) Wats., a native species of eastern Texas, has more variation in HFA contents and is also self-fertile compared with the cross-pollinated *L. fendleri*. This species is being used in our breeding program as a donor parent to introgress traits into *L. fendleri* (Dierig et al., 2005). The high seed productivity, wide genetic variability, and good seed retention of *L. fendleri* makes it superior to other *Lesquerella* species for domestication.

The crop is planted in the fall, usually October in the southwestern U.S. Following germination, plants remain semi-dormant until late January. Plant cover of 50% occurs in mid-February when plants begin flowering and continue until June when water application is terminated. Complete crop coverage occurs by mid-March in Arizona. Flowers are cross-pollinated by bees and other insects (Dierig et al., 1993). Plants are harvested in June using standard combine equipment. Small seeds (0.6 g/1000 seed) contained inside siliques (pods) are formed indeterminately along inflorescences.

The indeterminate flowers are dependent on environmental conditions such as irrigation and temperature. Studies by Windauer et al. (2004) indicated a linear response of temperatures that triggered the developmental stages of *L. fendleri*. They reported that *L. fendleri* growth increased linearly with temperature from emergence to bud appearance over a range of 9–20 °C in plants grown at constant temperatures in growth chambers. A broader range of temperatures, 9–24 °C, was required for the next phase of flower bud appearance to open flowers.

Many *Lesquerella* species follow a similar growth pattern where the flowering stage is dependent on water availability and temperatures (Rollins and Shaw, 1973; Nixon et al., 1983). Many plant growth characteristics and phenology of plants at different localities are influenced by environmental factors such temperature, moisture, and soil type. Ploschuk et al. (2001) observed that the duration of the flowering stage was lengthened by up to 15 days by water stress, but the number of stems produced was reduced. The objective of this study was to define regions of optimum production for lesquerella by determining the effect of temperature as imposed by varying elevation on plant phenology, growth characteristics, and seed yield of the two species, *L. fendleri* and *L. pallida*.

2. Materials and methods

The experiment was conducted at Phoenix, Tucson, Saffard, and Patagonia, Arizona. These four sites were selected primarily for elevation differences (Table 1). Seedlings were transplanted into the field from greenhouse seeded, eight-week-old plants on 12 November 2003 at Phoenix, 13 November 2003 at Patagonia, and 18 November 2003 at Tucson and Safford. Each location was planted in a randomized complete block design with 40 plants per plot and 8 replications. The greenhouse transplants were grown in Speedling polystryene trays (Speedling Inc., Sun City, FL, USA) with 72 cells, 5.5 cm × 5.5 cm × 7 cm per tray. Transplants were planted in rows 1 m apart and 0.36 m between plants in the row. *L. fendleri* seed used in this study was from a previously released public germplasm line, WCL-LY2 (Dierig et al., 2001), selected for high seed oil content and seed yield. Seed of the other species used in this study was labeled as *L. pallida* and originated from San Antonio Botanical Gardens, San Antonio, TX (accession A3219). However, chromosome numbers, oil quality, and some morphological traits distinguished it from this species and it still has not been taxonomically classified (unpublished data). Therefore, we refer to it as '*L. pallida* aff.' because although it has an affinity to *L. pallida*

Table 1
Location of sites selected in Arizona based on elevation differences and the minimum and maximum temperature for the growing season

Location	Latitude longitude	Elevation above sea level (m)	Temperature (°C)	
			Minimum	Maximum
USDA, ARS, U.S. Water Conservation Laboratory, Phoenix, AZ	33°39′N, 112°03′W	300	−1.1	38.8
The University of Arizona, Tucson Agricultural Center, Tucson, AZ	32°25′N, 110°95′W	700	−7.7	36.4
The University of Arizona, Safford Agricultural Center, Safford, AZ	32°83′N, 109°70′W	884	−9.1	33.7
Native Seeds/Search, Conservation Farm, Patagonia, AZ	31°54′N, 110°75′W	1219	−13.2	33.2

we are unsure of its taxonomic identification. The seeds originated from a wild collection and were unselected for any traits.

Weather data were collected weekly from the Arizona Meteorological Network (AZMET) for the Tucson and Safford locations. An AZMET station was not located at Patagonia so data were obtained from the National Audubon Society, Appleton–Whittell Research Ranch weather station at Elgin, AZ, approximately 30 km northeast of Patagonia. The Phoenix location utilized data from Phoenix Sky Harbor Airport, Office of the State Climatologist for Arizona, instead of the AZMet station in Phoenix because this location was closer in proximity and more representative of the field site. Data from these stations included the average minimum and maximum temperatures (Table 2), daily average temperatures, and precipitation.

Plant heights, plant widths (the average of north to south and east to west directions), and fresh and dry weights were measured beginning the first week of March and continued every two weeks until June at all locations. Plants were scored for the phenological stage of growth at the beginning of March and continued until plants were 100% in the fruit stage at each location. Ten plants were staked and scored in each of the eight replications as being in one of four stages that included (1) vegetative, (2) bud, (3) flower, or (4) fruit and expressed as a percentage. Plants at the Safford location had a high mortality rate possibly due to the high saline irrigation waters. As a result, fewer plants were scored for phenology, height, and width. Eighty plants (10 plants × 8 replications) were used at the other three locations for height and width measurements for each species from a single location. The Safford *L. fendleri* plants had only 44% survival and *L. pallida* aff. plants had only 10% by 02 May 2004.

Either one or two plants per plot of those not staked were harvested for fresh and dry weight at each measurement period every two weeks at each location. Final harvests were made from the four locations during the first week of June 2004 when the 10 staked plants per plot were harvested. Two of the 10 from each plot were used to determine plant fresh and dry weights and the remaining eight were used for single plant analysis of seed yield and seed oil traits.

Fresh and dry weights were determined by digging the whole plants and weighing them at the site. Plants were oven-dried at 70 °C for 48 h and re-weighed. Total seed oil content was measured non-destructively using 0.5 g of whole seeds from individual plants with a calibrated MQ20 Pulsed NMR analyzer (Bruker Biospin Corp., Billerica, MA, USA) and expressed as the percent of dry mass calculated by the instrument. Averages and standard errors were also calculated. Fatty acid contents

Table 2
High and low temperatures each month during the 2003–2004 growing season at the four sites in Arizona

Locations	Mean maximum and minimum temperatures (°C)							
	October	November	December	January	February	March	April	May
Phoenix (300 m)	28.7–13.1	22.2–7.0	20.3 to 3.5	20.2–5.2	18.6 to 4.7	29.1–11.8	28.5–12.9	35.3–17.1
Tucson (700 m)	27.9–11.5	22.4–5.5	20.2 to 0.4	18.6–3.0	17.9 to 1.1	26.8–9.6	26.4–10.0	33.8–14.2
Safford (884 m)	27.3–4.7	20.6–3.1	16.5 to −1.5	16.2–0.4	17.0 to −1.4	24.9–7.2	25.7–7.9	33.7–12.4
Patagonia (1219 m)			14.8 to −3.7	14.4–0.1	14.5 to −2.8	22.2–5.0	21.8–5.4	29.1–10.0

Data not available for Patagonia during October and November.

were determined with an HP 5890 gas chromatograph (Agilent Technologies, Willmington, Delaware, USA), with a non-polar 30 m × 0.22 mm column using a half-seed technique (Isbell et al., in preparation). One seed from each of the eight plants of each plot harvested in June was analyzed. From each sample, 4 μl was injected using an autosampler. The injection port temperature was 250 °C, the final oven temperature was 265 °C, and the FID detector was 250 °C. The carrier gas was helium at a pressure of 641 kPa.

Plot means were analyzed using SAS Proc Mixed (Littell et al., 1996). Log transformation of plant height, fresh weight, dry weight, and seed yield, and square root transformation for plant width were necessary to stabilize the variances among weeks, locations, and species. The model for plant height and weight and fresh and dry weight considered week, location, and species as fixed effects, and reps within location and line × reps within location as random effects. Fit statistics were used to select the covariance structure for the repeated measures across weeks among none, first-order autoregressive, or banded toeplitz. The model for seed yield, oil content, and fatty acid profile was simplified without the repeated measures. The probability of <0.05 was chosen for the level of significance. Student's *t*-tests were used to compare locations within species and weeks. Least squares means and 95% confidence intervals were transformed back to the original units of measurement for presentation in the figures.

3. Results and discussion

3.1. Phenological development

3.1.1. Lesquerella fendleri

Minimum and maximum temperatures decreased as the elevation increased at these four Arizona sites (Table 2). The lowest temperatures occurred on the same day (28 December 2003) for all four sites of −3.3 °C (Phoenix, 300 m), −7.7 °C (Tucson, 700 m), −9.1 °C (Safford, 884 m), and −13.2 °C (Patagonia, 1219 m). Plants had between 12 and 16 leaves and no branching at that date. The maximum temperatures occurred near harvest time on 05 June 2004 when temperatures rose to 41.5 °C (Phoenix), 40.3 °C (Tucson), 40.0 °C (Safford), and 36.1 °C (Patagonia). The final irrigation was applied at all sites by the middle of May and plants began drying for harvest by this time.

By 07 March 2004, the *L. fendleri* plants were all flowering at Phoenix. However, only about one-half of the plants at Tucson were in flower (Table 3A). Mean temperatures at Phoenix ranged between 4.7 and 18.6 °C for the month of February. There was little change in either the mean maximum or the highest temperature for

Table 3
Phenological stages of (A) *L. fendleri* and (B) *L. pallida* aff. plants at the four elevation sites in Arizona

Location	Date	Stage (% of total plants scored)							
		(A) *L. fendleri*				(B) *L. pallida* aff.			
		Vegetative	Bud	Flower	Fruit	Vegetative	Bud	Flower	Fruit
Phoenix	07 March	0.0	0.0	100.0	0.0	100.0	0.0	0.0	0.0
Tucson	07 March	1.0	34.0	64.0	0.0	100.0	0.0	0.0	0.0
Safford	07 March	31.2	65.0	3.7	0.0	100.0	0.0	0.0	0.0
Patagonia	07 March	83.1	16.9	0.0	0.0	100.0	0.0	0.0	0.0
Phoenix	21 March	0.0	0.0	0.0	100.0	83.7	15.0	1.2	0.0
Tucson	21 March	0.0	0.0	2.5	97.5	10.0	52.0	38.0	0.0
Safford	21 March	0.0	10.9	89.1	0.0	100.0	0.0	0.0	0.0
Patagonia	21 March	13.0	44.2	40.3	0.0	58.7	41.2	0.0	0.0
Phoenix	04 April	0.0	0.0	0.0	100.0	3.8	15.2	29.1	51.9
Tucson	04 April	0.0	0.0	0.0	100.0	0.0	0.0	2.5	97.5
Safford	04 April	0.0	0.0	3.5	96.5	46.1	46.1	0.0	7.7
Patagonia	04 April	2.8	5.6	43.1	47.2	47.5	51.2	1.2	0.0
Phoenix	18 April	0.0	0.0	0.0	100.0	0.0	0.0	0.0	100.0
Tucson	18 April	0.0	0.0	0.0	100.0	0.0	0.0	0.0	100.0
Safford	18 April	0.0	0.0	0.0	100.0	11.1	0.0	55.6	33.3
Patagonia	18 April	1.5	0.0	2.9	95.6	0.0	15.2	27.8	57.0

The percentage indicates the number of plants that had reached the respective stage at the various dates. When plants progressed to the next stage, they were no longer counted in the previous stage.

November to February at Phoenix. There was more of a difference in the minimum temperatures, which were starting to rise at Phoenix. Tucson temperatures were lower than Phoenix. Only a few plants at Safford and Patagonia were in flower at this time. Most of the Patagonia plants were still in the vegetative stage.

Two weeks later on 21 March, plants had already flowered and contained fruits (siliques) on almost all plants at Tucson as the minimum temperatures rose from 9.6 to 14.2 °C. The Phoenix plants all had fruits present on them at this date. All plants in Safford either had flower buds or flowers by 21 March. A few plants at Patagonia still remained vegetative, and the remainder had either buds or flowers. During this period of mid- to late-March, temperatures increased rapidly across Arizona. For the first week of March, temperatures were 7.2 °C for the mean minimum temperature and 18.3 °C for the average high temperature at Phoenix, and the following week, temperatures quickly rose to 12.8 °C for an average low and 31.7 °C for the average high. The same trend followed across the other elevation sites, stimulating growth stages at all locations.

The plants at three sites, Phoenix, Tucson, and Safford were at or near 100% in fruit by 04 April. Plants at Patagonia at this time were either flowering or fruiting. Plants did not reach near 100% until 18 April, almost one month later than Phoenix and Tucson.

These data agree with the growth chamber data of *L. fendleri* plants by Windauer et al. (2004) whose plants followed a linear increase of ontogeny in the field as temperatures increased. With lower elevations, the earlier plants of this species progressed into the next phenological stage. The plants appeared to be more sensitive to the minimum temperatures than to the maximum temperatures for this species.

3.1.2. *Lesquerella pallida aff.*

L. pallida aff. plants were slower to develop at these sites than *L. fendleri* plants (Table 3B). Plants did not progress from vegetative to bud stage until the week of 21 March at all locations except Safford where plants remained vegetative.

The plants at Tucson and Patagonia were further developed than those at the other sites 07 March and 21 March measurement periods. Some plants at Tucson already began to flower by 21 March (38%) even though temperatures had risen at about the same rate as the other sites. The maximum temperatures for both of these locations were similar. Minimum mean temperatures were between 3 and 4 °C cooler in Tucson than Phoenix and even lower on a number of individual days in February.

At the following measuring period of 04 April, plants at Phoenix surpassed those at Patagonia with 52% containing fruits. The Patagonia plants were either in vegetative or bud stages, except for one plant in flower. The plants there appeared to have more biomass and looked more productive than those at Phoenix. However, they developed quicker over their developmental stage at Phoenix presumably due to the warmer temperatures. The cooler temperatures at Patagonia may have been critical for prolonging each stage of development and biomass production of this species.

Most plants at Safford and Patagonia were flowering and many were in fruit by 18 April. Plants did not reach 100% fruiting until 02 May at these sites (data not shown) compared with Phoenix and Tucson plants with 100% fruit by 18 April.

The two species differed in their phenological responses. The *L. fendleri* plants responded linearly to warmer minimum temperatures, whereas *L. pallida* aff. plants had a less direct response. The *L. pallida* aff. plants remained in the vegetative stage longer throughout the season than *L. fendleri*. Plants in Tucson and Patagonia both formed buds earlier than at Phoenix and did not seem to be as sensitive to warmer temperatures. Plants at the warmer temperatures reached maturity faster than those at the higher, cooler elevations. However, plants began to change from the vegetative to bud stage at all sites about the same time. Possibly, floral induction in this species is dependent on other environmental signals, such as daylength, as speculated for *L. mendocina* by Windauer et al. (2004).

3.2. *Plant height, plant widths, and biomass during development*

3.2.1. *Lesquerella fendleri*

Height, width, and dry weight of *L. fendleri* all followed the same pattern throughout the season (Figs. 1A, 2A, and 3A). Plants at Phoenix (300 m) and Tucson (700 m) were similar, and those at Safford (884 m) and Patagonia (1219 m) were similar. Plants at Phoenix and Tucson were significantly larger than those at Safford and Patagonia.

Height and width of plants at Phoenix and Tucson increased at a rapid rate until 18 April when only small increases were observed (Figs. 1A and 2A). The 16 May period was the only exception where a significant difference in plant height was observed between the Phoenix and Tucson locations although plant heights at the following period two weeks later were not significantly different. It is unclear why this anomaly occurred. Plant widths were only different between the two locations on

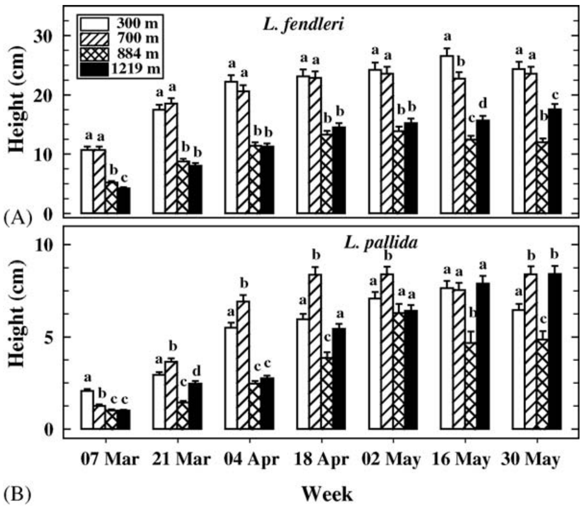

Fig. 1. Plant heights of (A) *L. fendleri* and (B) *L. pallida* aff. at Phoenix (300 m), Tucson (700 m), Safford (884 m), and Patagonia (1219 m) over seven measurement periods. Bars within the same week of measurement followed by different letters (a–d) are significantly different at the $P < 0.05$.

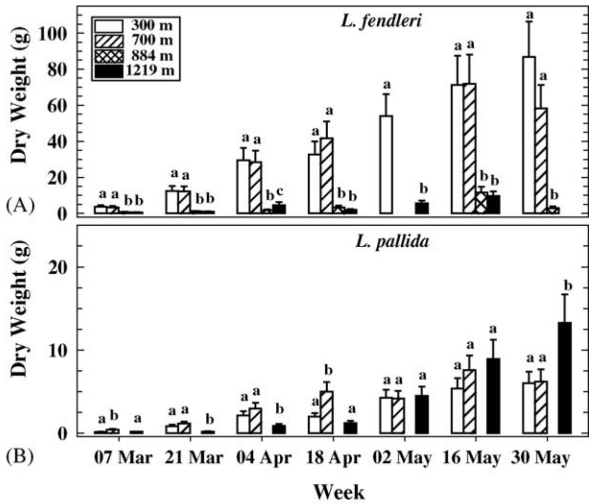

Fig. 3. Dry weights of (A) *L. fendleri* and (B) *L. pallida* aff. at Phoenix (300 m), Tucson (700 m), Safford (884 m), and Patagonia (1219 m) over seven measurement periods. Bars within the same week of measurement followed by different letters (a–c) are significantly different at the $P < 0.05$.

the first measurement period. The dry weight increased until 02 May at Tucson and at Phoenix increased until final harvest (Fig. 3A).

Plant height and width at Safford and Patagonia exhibited the same trend as the Phoenix and Tucson locations with a few exceptions. Plants at Safford during the first week of measurements were significantly taller and wider than those at Patagonia (Figs. 1A and 2A). However, this was reversed between the two locations after 02 May until harvest when the plants were taller and wider at Patagonia than those at Safford. After 18 April, plants at the two sites did not add significantly to height, width, or biomass. The missing data bar on Fig. 3A at Tucson for dry weights from 02 May and Patagonia on 30 May were due to lost plant samples. The missing data bar for Safford from the 02 May date was due to lack of plants in the field for destructive sampling.

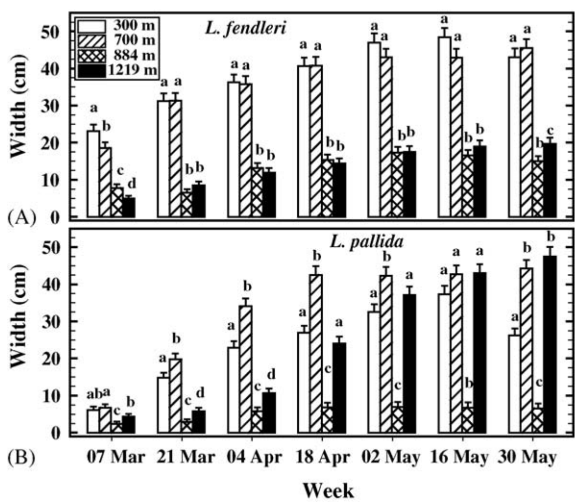

Fig. 2. Plant widths of (A) *L. fendleri* and (B) *L. pallida* aff. at Phoenix (300 m), Tucson (700 m), Safford (884 m), and Patagonia (1219 m) over seven measurement periods. Bars within the same week of measurement followed by different letters (a–d) are significantly different at the $P < 0.05$.

Biomass production of *L. fendleri* plants grown at elevations of 2900 m and above limited plant growth compared with plants grown at lower elevations. Plants grown at Phoenix and Tucson were significantly larger than plants at Safford and Patagonia by more than five-fold.

3.2.2. *Lesquerella pallida aff.*

Growth rates of *L. pallida* aff. plants followed much different trends than *L. fendleri* plants. Plants of *L. pallida* aff. at Tucson were taller and wider than plants at other locations in most weeks (Figs. 1B and 2B). Plants were taller at Phoenix at the first measurement in March. However, plants at Tucson surpassed them in height and width following this first period until 16 May when there was no significant difference between the two sites. By the end of the season, plants at Patagonia were equal to those in Tucson for height and width and higher values than those at the other two locations. The Safford plants were smaller than those at other sites throughout the season. This could be attributed to the high salinity at that location rather than to the higher elevation or temperature effect.

The Tucson plants had significantly higher dry weights than those at Patagonia until May (Fig. 3B). In two of the four periods before May, plants at Phoenix had heavier dry weights than those at Patagonia. However, plants at Patagonia during the first two May measuring periods were statistically the same as those at Tucson and Phoenix. Dry weights at Patagonia were higher than those at Phoenix and Tucson at final harvest.

Plants at Tucson and Phoenix became more brittle than the other sites as temperatures increased in late April and May and more difficult to harvest without loss of plant material. Plants at Tucson continued growth in height and width until 18 April and in biomass until 02 May. The Phoenix and Patagonia plants continued to increase in height, width, and biomass until 16 May. Plant dry weight continued to increase until the final harvest at Patagonia.

Temperature affected plant growth of *L. pallida* aff.; however, as with phenology, not as linearly as in *L. fendleri*. The warmer temperatures stimulated growth in early stages, but as temperatures increased, the plants at the highest elevation surpassed those at the lowest, indicating a narrower temperature range for plant growth with this species. Growth was hindered at Safford by salinity.

3.3. Final seed and oil yield harvest data

3.3.1. Lesquerella fendleri

The seed yields of plants at Phoenix and Tucson were not statistically different from each other, as were yields of plants at Safford and Patagonia (Table 4A). However, plants at Phoenix and Tucson were different than those at Safford and Patagonia. Seed yields closely followed the trend of dry weights of plants throughout the growing season for this species.

The oil contents were similar for plants at all four sites (Table 4A). The Safford plants had significantly lower oil content than the other three sites, but not by a large margin. The quality of the seed analyzed from this site was affected by the poor growing conditions, possibly due to the high salinity at Safford. This resulted in lower oil values. The similarities in oil contents between the sites indicated little environmental effect due to temperature for this trait. Ploschuk et al. (2003) reported that plants sown in the fall and spring had significant differences in oil content in Argentina. The germplasm used in that experiment was an unimproved wild accession with higher variability for oil content compared with the selected germplasm line used in our study. It is unclear as to why these differences were observed.

The lesquerolic acid (C20:1-OH) content was also unaffected by elevation at the three sites, Phoenix, Tucson, and Patagonia (Table 5A). Seed was not available for replicated analysis at Safford. The other fatty acids analyzed were also not significantly different between the sites. The oil quality of this species appears to be unaffected by environmental influences occurring at these four sites.

Ploschuk et al. (2003) did not measure this trait in their study. However, studies of other oilseeds such as canola (*Brassica napus*) reported strong environmental influence on seed oil fatty acids, especially linolenic acid (Somers et al., 1998). This indicates that selection of lesquerella for higher or lower content of these fatty acids would be possible providing adequate variability exists (Dierig et al., 1996).

3.3.2. Lesquerella pallida aff.

The Patagonia site had the largest plants at final harvest (Fig. 3B) and the highest seed yields (Table 4B) of all locations, although not statistically different than Tucson. Yields could have been higher at Tucson, but as mentioned earlier, the plants dried out early due to high temperatures, became brittle and difficult to harvest. Some seed shattering occurred. This was also because drip irrigation was used to accommodate the small plots

Table 4
Average seed oil content and seed yields of (A) *L. fendleri* and (B) *L. pallida* aff. at final harvest from the four field sites

Location	(A) *L. fendleri*		(B) *L. pallida* aff.	
	Oil content (%)	Seed yield per plant (g)	Oil content (%)	Seed yield per plant (g)
Phoenix (300 m)	30.1 a	10.93 a	17.6 ab	0.11 a
Tucson (700 m)	30.3 a	12.65 a	23.5 b	0.16 ab
Safford (884 m)[1]	28.0 b	1.23 b	–[1]	–[1]
Patagonia (1219 m)	29.3 ab	1.24 b	19.6 a	0.24 b

Different letters (a and b) in the same column indicate significant difference for each variable of both species ($P < 0.05$).
[1] Data not available due to lack of adequate seed at harvest.

Table 5
Average fatty acid content of seed oil profiles of (A) *L. fendleri* and (B) *L. pallida* aff. at final harvest from the four field sites

	C16:0 Palmitic (%)	C16:1 Palmitoleic (%)	C18:0 Stearic (%)	C18:1 Oleic (%)	C18:2 Linoleic (%)	C18:3 Linolenic (%)	C20:1-OH Lesquerolic (%)
(A) *L. fendleri*							
Phoenix	0.945 a	1.35 a	1.68 a	14.82 a	7.14 a	12.85 a	60.83 a
Tucson	0.936 a	1.37 a	1.88 a	17.34 a	6.54 a	12.65 a	59.20 a
Safford[1]	–	–	–	–	–	–	–
Patagonia	0.933 a	1.43 a	1.91 a	15.47 a	6.75 a	12.22 a	59.72 a
(B) *L. pallida*							
Phoenix	2.64 a	2.70 a	2.79 a	15.65 a	16.85 a	5.60 a	51.51 a
Tucson	1.98 b	1.78 b	2.0 b	13.18 a	11.70 b	5.16 a	62.70 b
Safford[1]	–	–	–	–	–	–	–
Patagonia	1.93 b	1.76 b	2.14 b	14.08 b	12.35 b	4.93 a	61.76 b

Different letters (a and b) in the same row indicate significant difference for each variable ($P < 0.05$).
[1] Data not available due to lack of adequate seed at harvest.

and caused plants to have shallow root systems compared to plants in a commercial planting with flood irrigations.

Oil content was statistically different at all three locations (Table 4B). It was highest at Tucson, lowest at Phoenix, and intermediate at Patagonia. It is not clear whether the oil content in this species was influenced by temperature because it did not correspond to the elevation gradient. Lesquerolic acid (C20:1-OH) was significantly different between the Phoenix and Tucson, but not between Tucson and Patagonia (Table 4B). The same trend was observed for fatty acids C16:0, C16:1, C18:0, and C18:2. Values of oleic acid (C18:1) were significantly different only between Phoenix and Tucson locations and no differences between locations for values of linolenic acid (C18:3). The range of production where *L. pallida* aff. grew best was at sites between 800 and 1219 m. The exception to this was where salinity confounded the temperature effects as experienced in Safford.

4. Conclusion

Temperature and elevation effects were pronounced on traits such as height, width, fresh and dry weights, and seed yields of both species. The phenology *L. fendleri* followed a linear response to temperature. As temperatures increased, plants progressed to the next stage of growth and reproduction. Temperature did not have as much impact on *L. pallida* aff. as *L. fendleri* for phenology. Plants may be more dependent on other environmental signals for floral induction of this species such as vernalization.

Plants of *L. fendleri* followed similar trends as *L. pallida* aff. in fresh and dry weights at final harvest as occurred during the growing season. Plants at the two lower elevations, Phoenix and Tucson, were statistically the same in biomass. They both produced more biomass and seed yield than those at the other two sites, Safford and Patagonia. Plants at these sites were also not statistically different from each other. Oil content and oil profile were relatively stable over the four environments for *L. fendleri* indicating selection may be relatively easy provided the genetic diversity is present. *L. fendleri* was more adapted to elevations below 700 m. The effect at elevations between 700 and 884 m is not clearly understood. Biomass production and seed yield dropped dramatically at the higher elevations (884 and 1219 m).

Biomass production and seed yields of *L. pallida* aff. were highest at Patagonia and Tucson. The trends for plant dry weight changed over the season. Plants started out with higher values at the two lower elevations. The highest elevation site by April was equivalent in dry weight to the lowest site. At final harvest, plants produced more biomass at Patagonia than either Phoenix or Tucson. Seed yields were also greatest at Patagonia. Oil content and oil profile were variable across the sites.

L. pallida aff. is native to a narrow geographic locality in eastern Texas associated with a wetter habitat than *L. fendleri*, although the elevation of the native sites is only between 45 and 125 m. *L. fendleri* is found at elevations above 1500 m, but production appears to be more suitable at the lower elevations. Because breeding efforts have begun to incorporate traits from *L. pallida* aff. into *L. fendleri*, this production range may be expanded with hybrids of the two species.

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