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Variation of seed oil composition in parent and S_1 generations of *Lesquerella fendleri* (Brassicaceae)[☆]

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Abstract

The seed oil of *Lesquerella fendleri* is valued for its use in industrial products including lubricants, methyl esters for diesel fuel additives, greases, drying agents, plastics, nylon-11, surfactants and protective coatings. The predominate fatty acids in the seed oil of all *Lesquerella* species are hydroxy fatty acids (HFA) and the HFA found in *L. fendleri*, the species being developed as a new crop for the southwestern U.S., is lesquerolic acid. The amount of variability for this and other fatty acids in its seed oil profile was considered somewhat narrow, limiting the potential progress in breeding for oil quality traits. A half seed method (HSM) of fatty acid analysis adapted for this small-seeded species, where the mean seed weight is 0.006 g, when compared to a bulk seed method (BSM) shows that much diversity actually exists. This variability was masked because the BSM is an average value of up to 50 seeds for each analysis compared to a half of a seed that results from a single pollination event. One thousand HSM seeds from an improved breeding population, WCL-LO3 were analyzed and the same breeding population analyzed by the BSM. A population of 32 unimproved accessions was also included for comparison because it represents the most diverse germplasm available for *L. fendleri*, originating from several geographical locations. Greater variability was detected with the HSM, especially for lesquerolic acid. Plants with lesquerolic acid values up to 74% and as low as 36% were found by the HSM, compared to an average of 55% by the BSM. These are the highest values reported for lesquerolic acid in this species. Lower values for two acids causing high oxidative instability of the oil, linoleic and linolenic were also detected. Plants with high and low lesquerolic acid values were then selected and S_1 populations produced. The means from these 'high' and 'low' selected progeny populations were not the same as the respective mean parental values. The variability in these progeny was similar to the range and mean observed in the original population. This is likely due to at least a couple of genes segregating for this trait, requiring further generations for improvement and to determine the genetic inheritance of fatty acid.

Keywords: Genetic variability; Hydroxy fatty acids; Lesquerolic acid; Seed oil composition

1. Introduction

The unusual seed oil composition of *Lesquerella fendleri* (Gray) Wats., native to the southwestern U.S. and northcentral Mexico, was recognized almost 50 years ago during a massive screening by the USDA, Agricultural Research Service of nearly 200 plant families (Jones and Wolff, 1960). Many plant species were discovered at that time as having possible applications for industrial uses and the genus *Lesquerella* was found to

☆ Names are necessary to report factually on available data; however, the USDA neither guarantees nor warrants the standard of the product, and the use of the name by USDA implies no approval of the product to the exclusion of others that may also be suitable.

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have an exceptional seed oil composition, compared to most others being screened (Barclay et al., 1962).

The unusual hydroxy acid found in the plant's seed oil was named lesquerolic acid or 14-hydroxy-eicosa-*cis*-11-enoic acid (C20:1OH) (Smith et al., 1961). The oil was similar to oil of castor (*Ricinus communis* L.), which is composed of mostly ricinoleic acid or 12-hydroxy-octadeca-*cis*-9-enoic acid (C18:1OH). The biosynthetic pathways by which the two fatty acids are derived are similar; both plants convert oleic acid, C18:1 to C18:1OH, ricinoleic acid through hydroxylation (van de Loo et al., 1995; Engeseth and Stymne, 1996; Morris, 1997). Reed et al. (1997) determined that lesquerolic acid is then synthesized through the elongation of C18:1OH to C20:1OH. The oleate hydroxlase gene, that converts C18:1 to C18:1OH, has been cloned from castor (CFAH12) (van de Loo et al., 1995) and from *L. fendleri* (LFAH12) (Broun et al., 1998a).

Lesquerella oil has many potential industrial uses that include biolubricants, methyl esters for diesel fuel lubricity, nylon-11, greases, drying agents, paints and varnishes, surfactants, coatings and cosmetics (Roetheli et al., 1991). Many of the formulations of these products are distinct from castor oil due to difunctional instead of trifunctional moieties of the hydroxy triglycerides (Cermak et al., 2006). Capturing some of these markets for lesquerella oil will require achieving the highest possible levels of lesquerolic acid and low levels of unsaturated fatty acids.

In other crops such as rapeseed (*Brassica napus*), adequate amounts of natural variability for oil composition has been found (Stefansson and Hougen, 1964). In contrast, many other cultivated oilseed crops have low variability for improvement unless induced by mutagenesis or genetic engineering (Rattray, 1991; Velasco et al., 1999). A half seed method (HSM) has been described in other oilseed crops for fatty acid analysis (Knowles, 1989) and has provided benefit to breeding programs where the crops produce more than one seed per fruit such as rapeseed, safflower, or sunflowers. The genetic inheritance of seed oil traits of individual seed can then be determined because the source of pollination can be traced. This method also allows for detection of mutations for these traits and the improvement through plant breeding for seed oil quantity and quality. The small seed size of *L. fendleri* (0.006 g) required a destructive seed analysis of up to 50 seeds for a bulk seed method (BSM) representing a serious impediment to breeding improvement for oilseed traits. Recently, the HSM of analysis was adapted for this crop (Isbell et al., in press). The objective of this research was to re-examine the amount of variability of *L. fendleri* for fatty acid content based on a HSM compared to a BSM, in hope of using this variability to shorten the domestication process and provide diverse oilseed phenotypes for future breeding and inheritance studies.

2. Materials and methods

In 2004–2005, randomly selected seeds from a released germplasm line of *L. fendleri*, WCL-LO3 (Dierig et al., 2006b) were analyzed for oil profile by a BSM and HSM. Thirty-two unimproved accessions of *L. fendleri*, representing the most diverse population available (Salywon et al., 2005) were also analyzed by BSM. This germplasm originated from native locations across the southwestern U.S. and Mexico and then were grown for seed increase at this laboratory under field conditions.

The HSM entailed cutting a seed with a scapel and analyzing the fatty acid methyl esters from the distal portion of the cotyledons. The other half of the seed with the proximal portion of the cotyledons and the entire hypocotyl was planted in a Petri dish with potting soil and germinated in growth chambers at 25 °C for 16 h day temperature and 15 °C for 8 h night temperature. The remaining portion of the seed was used to determine the fatty acid composition of seed lipids on a HP 5890 series II (Hewlett-Packard, Palo Alto, CA) gas chromatograph (GC) with a nonpolar 30 m × 0.22 mm i.d. column (Isbell et al., in press). A known source of *L. fendleri* seed oil was run as a standard for comparison. The BSM entailed using up to 50 random seeds crushed together and analyzed on the same gas chromatograph using a polar 30 m × 0.25 mm. i.d. column as described in Dierig et al. (1996).

There were 1000 WCL-LO3 seeds analyzed by the HSM and 20 replications of 20 seeds of the same line bulked together for the BSM. The seed source used for both methods of this line was harvested from field grown plants under irrigated conditions in 2004. The criterion for selection of S_0 plants from the HSM was based on lesquerolic acid content. Those above 62% were selected as 'high', representing 15% of total population and those below 53 for 'low', representing 10% of the total population. The 32 accessions were analyzed by combining between one and four replications of up to 50 seeds per accession, depending on the seed amount available from each accession, which were produced from field grown plants. The mean of all 32 accessions were averaged.

Half seeds were planted in the growth chamber and then transplanted into 10 cm plastic pots and moved to a greenhouse. Many selected seeds did not germinate and some plants did not survive from growth chamber to greenhouse. Plants were self pollinated by bud pollination in the greenhouse between December 2004 and April 2005 and 5 cm × 18 cm glassine bags placed over the inflorescences until maturity. The S_1 seed resulting from self pollinations were also analyzed by the HSM. There were between 40 and 80 seeds from high and low selections analyzed.

3. Results and discussion

3.1. *L. fendleri* fatty acid profile

More variability was found in fatty acid content of the WCL-LO3 line analyzed by the HSM than in either WCL-LO3 or the 32 accessions analyzed by the BSM (Table 1). The least variability was found when WCL-LO3 was analyzed by BSM. In a previous study by Salywon et al. (2005), the same 32 unimproved *L. fendleri* accessions were used in the analysis of the fatty acid composition, using the BSM. They are included herein since they represent a broader range of variability of *L. fendleri* than the single breeding line, WCL-LO3, having originated from a number of geographical locations without selection. The BSM of WCL-LO3 provided a direct comparison to the same line analyzed with the HSM. As expected, the unimproved accessions were more variable than WCL-LO3 when both were analyzed by the BSM; the WCL-LO3 line had been selected for oil content, resulting in a more uniform population.

The predominant fatty acid, lesquerolic acid, contained between 35.8 and 74.0% when analyzed by the HSM, where the BSM seeds had an upper range of only 56.1 and 58.2% (Table 1). Although the lower range value for the BSM unimproved accessions was lower for the same trait compared to the HSM, the range was still greater from the HSM. The lower value was possibly due to the adverse effect of immature seeds contained in the mix of bulk seeds analyzed and may not represent the true genotypic variation (Salywon et al., 2005). The variability uncovered by the HSM for this acid provides an opportunity for breeding to improve this trait. Forty six percent of those analyzed by the HSM contained ≥60% lesquerolic acid, 9% contained ≥64% and 1% contained ≥70%. These are the highest values reported for lesquerolic acid in this species and indicate that more natural variability exists than previously reported (Dierig et al., 1996; Salywon et al., 2005). It has been reported that *L. fendleri* in most cases excludes the lesquerolic acyl from the *sn*-2 position of the triglyceride (Hayes et al., 1995). This accounts for the upper limit of the range for lesquerolic acid being near two-thirds or 67% for the seed fatty acid content since two of the three positions potentially contain one lesquerolic acid molecule. The 1% of the seeds with values ≥70 may have contained some portion of triacylglycerols with lesquerolic acyl groups in all three of the *sn* positions. Castor has this ability and produces ricinoleic acyl groups in all three *sn* positions almost 100% of the time. There is also a possibility that another HFA, auricolic acid (C20:2OH), may not have separated sufficiently from the lesquerolic acid peak on the gas chromatograph, nonpolar column used for this study. This acid would only account for approximately 1–5% of the total fatty acid content (Dierig et al., 1996; Salywon et al., 2005). A few *Lesquerella* species have the ability to produce lesquerolic acid in quantities above the two-thirds level (Dierig et al., 2004).

It would be desirable in many industrial applications to eliminate or significantly reduce levels of two unsaturated fatty acids, linoleic and linolenic acids, present in lesquerella oil which causes low oxidative stability.

Table 1
Means and ranges for fatty acid composition for (a) improved line WCL-LO3 by half seed method (HSM); (b) improved line WCL-LO3 by bulk seed method (BSM) and (c) 32 unimproved accessions by BSM

	C16:0 palmitic (%)	C16:1 palmitoleic (%)	C18:0 stearic (%)	C18:1 oleic (%)	C18:2 linoleic (%)	C18:3 linolenic (%)	C20:1OH lesquerolic (%)
(a) HSM WCL-LO3							
Mean $n = 1000$	0.83	1.27	1.9	19.9	6.6	11.7	59.9
Range	0.1–6.2	0.5–5.80	1.9–12.4	6.7–33.2	0.3–14.5	5.1–19.2	35.8–74.0
(b) BSM WCL-LO3							
Mean $n = 20$	1.1	0.56	1.6	15.5	7.9	12.4	54.5
Range	1.0–1.2	0.41–0.67	1.4–1.8	14.7–16.3	7.0–8.5	11.8–13.1	53.0–56.1
(c) BSM-unimproved accessions							
Mean $n = 80$	1.5	0.3	2.4	17.7	8.4	13.8	51.4
Range	0.9–3.4	0.0–1.7	1.6–3.1	14.8–28.2	6.3–12.6	11.1–21.8	25.1–58.2

Although the means of both of these fatty acids shown in Table 1 were not significantly different between the two methods, the values at lower end of the range derived by the HSM were reduced by at least 5% of total oil compared to the BSM. Two percent of the HSM seeds had linoleic acid values below 4% and 2% had linolenic acid values below 8%. Differences were more apparent in the lower ends of the range of values. The values at the upper ends of the range from the BSM of the 32 variable accessions and the HSM were similar for both fatty acids. These acids are dependent on their precursor, oleic acid, which also had similar upper range limits for the HSM and the BSM of the 32 accessions.

Oleic acid is a precursor to lesquerolic acid (Reed et al., 1997; Broun et al., 1998b) and a negative correlation between the two would be expected. The coefficient of determination (r^2) from the HSM was −0.50. In castor, where oleic acid is the direct precursor to ricinoleic acid, Rojas-Barros et al. (2004) found a −0.99 correlation. The differences in the coefficients of determination between lesquerella and castor can be attributed to the partitioning of the catalytic specificity of the hydroxylase genes of the two taxa. The hydroxylase enzyme in *L. fendleri* has both hydroxylase and desaturase activities, in contrast to castor (Broun et al., 1998a,b). *L. fendleri* hydroxylates oleic acid to another HFA and then via elongation of primarily ricinoleic acid, lesquerolic acid is produced (Reed et al., 1997). The lower values of the range for oleic acid by the HSM found in Table 1 compared to the BSM resulted from the higher values for lesquerolic acid by the HSM. Low oleic acid values (below 11%) always corresponded to higher lesquerolic acid values (>65%). Since these high values were not found in seeds from the bulk method, the low oleic acid values were not detected either.

3.2. *S_0 and S_1 generations of high and low hydroxy fatty acids selections*

Selections made for low and high lesquerolic acid are shown in Table 2. The means for lesquerolic acid were between 40.1 and 52.8% for the 'low' selections and 62.4 and 73.4% for the 'high' selections. Other seeds had lower or higher values but did not survive. Values for other fatty acids were similar between 'high' and 'low' selections with a few exceptions. The stearic acid content of low HFA selection HS653 was 12.4% compared to other selections which were 3.5% and below. The oleic acid content values were higher in the 'low' selections compared to the 'high' selection due to oleic acid being a precursor to the acid being selected, indicating conversion to lesquerolic acid occurred at a lower rate.

Mean values for lesquerolic acid from either 'high' or 'low' selections (Table 3) were more similar to the total mean from the HSM (Table 1) than to the value of each parent. The selfed progeny from the 'high' selections produced seeds in the upper range and selfed seed from the 'low' selections produced seeds in the lower range that were similar to their respective parents. Seeds from the 'high' selections had seeds with lower values than those from the 'low' selections.

Cross pollination by insects is the normal mode of reproduction for *L. fendleri* since individual plants are self-incompatible. Plants in this study were self pollinated by bud pollination to circumvent incompatibility, resulting in segregation for these traits. Genetic control for lesquerolic acid content is likely due to either a couple or many genes. It is also possible that a single gene combined with environmental effects could be responsible. A previous study by Dierig et al. (2006a) indicated that environmental effects on oil profile in

Table 2
Fatty acid compositions of selections for high and low HFA analyzed by the HSM

	C16:0 palmitic (%)	C16:1 palmitoleic (%)	C18:0 stearic (%)	C18:1 oleic (%)	C18:2 linoleic (%)	C18:3 linolenic (%)	C20:1OH lesquerolic (%)
(a) Low HFA selections							
HS653	0.0	0.0	12.6	15.6	4.8	8.6	40.1
HS759	1.0	1.62	2.3	20.6	9.8	10.4	52.8
HS817	0.9	2.09	3.5	22.4	13.1	8.4	48.0
(b) High HFA selections							
HS163	0.98	0.8	0.98	10.0	7.3	8.2	71.7
HS183	0.64	1.01	1.2	10.1	6.4	7.9	72.1
HS617	0.80	0.80	0.92	11.0	4.2	12.8	68.9
HS853	0.55	0.70	0.87	9.6	3.0	11.1	73.4
HS884	0.85	0.84	0.99	11.8	3.7	10.8	70.1
HS927	0.5	1.22	1.4	15.3	5.5	12.6	62.4

Table 3
Means and ranges for fatty acid composition of S_1 generation high HFA selections

		C16:0 palmitic (%)	C16:1 palmitoleic (%)	C18:0 stearic (%)	C18:1 oleic (%)	C18:2 linoleic (%)	C18:3 linolenic (%)	C20:1OH lesquerolic (%)
(a) Low HFA selections								
HS653 $n=40$	mean	1.3	0.9	1.4	15.0	4.6	15.0	61.6
Range		0.0–2.1	0.6–2.0	0.8–2.4	10.0–19.5	3.4–6.8	12.0–15.3	54.6–71.5
HS759 $n=40$	mean	1.9	1.3	1.5	16.4	5.0	14.6	58.7
Range		1.0–3.7	0.7–5.2	0.9–2.2	12.4–20.1	3.5–8.5	12.5–17.1	50.5–65.2
HS817 $n=40$	mean	1.4	0.8	1.7	14.2	5.3	13.8	61.2
Range		1.0–1.9	0.6–1.3	1.2–2.1	11.0–16.0	3.9–7.4	11.0–15.1	55.4–67.1
(b) High HFA selections								
HS163 $n=80$	mean	1.5	1.0	1.5	14.7	5.0	11.8	58.5
Range		0.9–7.8	0.5–8.8	0.7–7.2	9.2–22.7	2.3–9.3	7.3–15.1	33.7–69.4
HS183 $n=60$	mean	1.4	1.0	1.5	14.9	4.7	13.07	61.3
Range		0.7–7.3	0.6–7.2	0.8–3.2	8.8–18.5	2.4–8.6	9.9–14.4	47.2–71.1
HS617 $n=40$	mean	1.4	1.0	1.6	15.1	4.7	13.6	60.0
Range		0.0–2.3	0.5–1.5	1.1–3.5	11.4–25.9	1.6–7.5	11.9–16.9	51.3–65.7
HS853 $n=40$	mean	1.3	1.2	1.5	13.3	3.3	14.9	60.2
Range		0.0–1.7	0.0–1.8	1.1–2.7	8.0–16.1	2.2–7.5	9.9–16.1	53.1–69.1
HS884 $n=80$	mean	1.5	1.5	1.5	15.1	3.5	13.27	58.1
Range		0.9–2.7	0.8–3.1	0.8–6.3	8.4–22.2	2.4–7.2	9.5–18.3	42.5–76.5
HS927 $n=40$	mean	2.0	1.2	1.3	15.0	5.6	13.1	59.1
Range		1.3–2.8	0.8–1.8	0.8–2.2	10.6–18.2	3.2–10.5	9.3–15.5	47.1–64.5

this species were low and not likely the reason for the discrepancy between the parent and selfed progeny. Plants grown under different temperatures as a result of high and low elevations were not significantly different in lesquerolic acid content. Further generations are required to produce a consistently high breeding line for this trait and to understand the exact control involved.

Most seeds had similar means and ranges for other fatty acids from either selection type (Table 3). The 'high' selection, HS163 had upper range values for C16:0 and C16:1 that were higher than normal. The same selection also had a lesquerolic acid value lower than any other selections. These three values all resulted from the same seed. The same was also true for the other 'high' selection, HS617, where all three values were the extremes of the respective ranges. The parent values of the three 'low' selections listed in Table 2 did not follow the same trend of high C16:0, C16:1 and low C20:1OH values.

The frequencies of individuals from lesquerolic acid values of the progeny from 'high' and 'low' selections (Fig. 1) have similar means, however, more individuals from 'high' selections fell into the upper end classes compared to those from 'low' selections. There were 18 (9%) 'high' selection seeds in classes 65% and above compared to 11 (8%) 'low' selections. Also, there were 27 (19%) individuals from 'low' selections below 50% lesquerolic acid compared to 12 (6%) from 'high' selection classes.

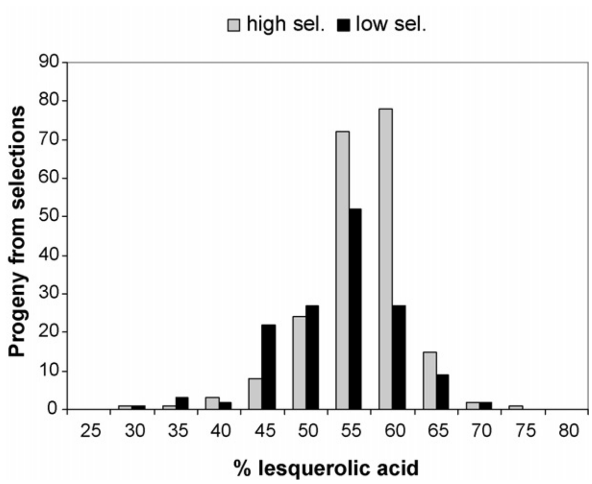

Fig. 1. Frequency distribution of lesquerolic acid values for the S_1 generation for high ($n=205$) and low ($n=145$) lesquerolic acid selections.

4. Conclusions

The study demonstrated that more natural variability exists than previously thought for the fatty acid profile of *L. fendleri*. The upper limits of lesquerolic acid in the seed oil of *L. fendleri* is likely limited by the ability to contain lesquerolic acyl groups in all three of the *sn* positions of the triglyceride molecule. Nevertheless, this may occur infrequently because some seeds contained up to 76% lesquerolic acid, which is higher than the theoretical limit of 67% for this species. It appears possible to develop *L. fendleri* cultivars with 70–75% lesquerolic acid content. This is substantially higher than the current improved line with 59%. Introgression of genes from other species or genera would be needed to go beyond that range, unless more variability within the species is found. There also appears to be more opportunity to decrease both linoleic and linolenic acids since variability was detected in this study at the lower ends of their ranges with the HSM. The elimination of linolenic acid does not seem likely. Seeds with values were found at 5% as the low end of the range. Seed with near 0% linoleic acid were found.

References

Barclay, A.S., Gentry, H.S., Jones, Q., 1962. The search for new industrial crops II: *Lesquerella* (Cruciferae) as a source of new oilseeds. Econ. Bot. 16, 95–100.

Broun, P., Shanklin, J., Whittle, E., Somerville, C., 1998a. Catalytic plasticity of fatty acidmodification enzymes underlying chemical diversity of plant lipids. Science 282, 1315–1317.

Broun, P., Bodupalli, S., Sommerville, C., 1998b. A bifunctional oleate 12-hydroxylase: desaturase from *Lesquerella fendleri*. Plant J. 13, 201–210.

Cermak, S.C., Brandon, K.B., Isbell, T.A., 2006. Synthesis and physical properties of estolides from lesquerella and castor fatty acid esters. Ind. Crops Prod. 23, 54–64.

Dierig, D.A., Adam, N.A., Mackey, B.E., Dahlquist, G.H., Coffelt, T.A., 2006a. Temperature and elevation effects on plant growth, development, and seed production of two *Lesquerella* species. Ind. Crops Prod. 24, 17–25.

Dierig, D.A., Tomasi, P.M., Dahlquist, G.H., 2006b. Registration of WCL-LO3 high oil *Lesquerella fendleri* germplasm. Crop Sci. 46, 1832–1833.

Dierig, D.A., Tomasi, P.M., Salywon, A.M., Ray, D.T., 2004. Improvement in hydroxy fatty acid seed oil content and other traits from interspecific hybrids of three *Lesquerella* species: *Lesquerella fendleri, L. pallida* and *L. lindheimeri*. Euphytica 139, 199–206.

Dierig, D.A., Thompson, A.E., Rebman, J.P., Kleiman, R., Phillips, B.S., 1996. Collection andevaluation of new *Lesquerella* and Physaria germplasm. Ind. Crops Prod. 5, 53–63.

Engeseth, N., Stymne, S., 1996. Desaturation of oxygenated fatty acids in *Lesquerella* and other oil seeds. Planta 198, 238–245.

Hayes, D.G., Kleiman, K., Phillips, B., 1995. The triglyceride composition, structure, and presence of estolides in the oils of *Lesquerella* and related species. J. Am. Oil Chem. Soc. 72, 559–565.

Isbell, T.A., Dahlquist, G.H., Dierig, D.A. A half seed method for fatty acid analysis in a small seeded *Lesquerella* species. Ind. Crops Prod., in press.

Jones, Q., Wolff, I.A., 1960. The search for new industrial crops. Econ. Bot. 14, 56–68.

Knowles, P.F., 1989. Genetics and breeding of oil crops. In: Downey, R.K., Röbbelen, G. (Eds.), Oil Crops of the World. McGraw-Hill, NY, pp. 361–374.

Morris, L.J., 1997. The mechanism of ricinoleic acid biosynthesis in *Ricinus communis* seeds. Biochem. Biophys. Res. Commun. 29, 215–311.

Rattray, J., 1991. Plant biotechnology and the oil and fats industry. In: Rattray, J. (Ed.), Biotechnology of Plant Fats and Oils, Am. Oil Chem. Soc., Champaign, IL, pp. 1–35.

Reed, D.W., Taylor, D.C., Covello, P.S., 1997. Metabolism of hydroxy fatty acids in developing seeds in the genera *Lesquerella* (Brassicaceae) and Linum (Linaceae). Plant Physiol. 114, 63–68.

Roetheli, J.C., Carlson, K.D., Kleiman, R., Thompson, A.E., Dierig, D.A., Glaser, L.K., Blase, M.G., Goodell, J., 1991. Lesquerella As a Source of Hydroxy Fatty Acids for Industrial Products. USDA-CSRS Office of Agricultural Materials, Washington, DC, U.S.A (growing industrial materials series (unnumbered)).

Rojas-Barros, P., de Haro, A., Mũnoz, J., Fernández-Martínez, J.M., 2004. Isolation of a naturalmutant in castor with high oleic/low ricinoleic acid content in the oil. Crop Sci. 44, 76–80.

Salywon, A.M., Dierig, D.A., Rebman, J.P., Jasso de Rodríguez, D., 2005. Evaluation of new Lesquerella and Physaria (Brassicaceae) germplasm. Am. J. Bot. 92, 53–62.

Smith, C.R., Wilson, T.L., Miwa, T.K., Zobel, H., Lohmar, R.L., Wolff, I.A., 1961. Lesquerolic acid A new hydroxy acid from Lesquerella seed oil. J. Org. Chem. 26, 2903–2905.

Stefansson, B.R., Hougen, F.W., 1964. Selection of rape plant (*Brassica napus*) with seed oil practically free from erucic acid. Can. J. Plant Sci. 44, 359–364.

van de Loo, F.J., Broun, P., Turner, S., Sommerville, C., 1995. An oleate 12-hydroxylase from *Ricinus communis* L. is a fatty acyl desaturase homolog. Proc. Natl. Acad. Sci., U.S.A. 92, 6743–6747.

Velasco, L., Perez-Vich, B., Fernández-Martinez, J., 1999. The role of induced mutagenesis in the modification of the fatty acid profile of oilseed crops. J. Appl. Genet. 40, 185–209.