TWO-YEAR STUDY ON THE INHERITANCE OF REDUCED SATURATED FATTY ACID CONTENT IN SUNFLOWER SEED

Brady A. Vick*, C. C. Jan, and Jerry F. Miller

U.S. Department of Agriculture, Agricultural Research Service, Northern Crop Science Laboratory, P.O. Box 5677, Fargo, ND 58105, USA

Received: August 10, 2004
Accepted: November 22, 2004

SUMMARY

RS1 and RS2 are two genetic stocks that have low saturated fatty acid (SFA) contents. In this two-year study, we report on the inheritance of palmitic and stearic acids of RS1 and RS2 in the F1 and F2 generations of crosses with HA 382, an inbred line with a fatty acid composition similar to many commercial sunflower hybrids. The expression of the reduced palmitic and stearic acid traits is most important in the F2 generation because it is the F2 seed that is harvested by the farmer, sold, and crushed for the oil. Our experiments showed that the F2 seed of reciprocal crosses of RS1 or RS2 with HA 382 was intermediate in SFA content between the two hybrid parents. The inheritance and expression of the reduced palmitic and stearic acid traits of RS1 and RS2 were controlled by more than one gene. In addition, there were significant relative changes in palmitic and stearic acid contents between the growing seasons of 2002 and 2003, suggesting that environment played a significant role in the relative proportions of these fatty acids. The total SFA content was also influenced by environment, producing opposite effects with RS1 (higher total SFA in 2003) and RS2 (lower total SFA in 2003). The data demonstrate that it will be necessary to incorporate the reduced SFA trait into both parents of a hybrid in order to achieve the lowest concentration of SFAs in the F2 seed.

Key words: F1 hybrid, Helianthus annuus, maternal effects, multigenic inheritance, palmitic acid, stearic acid

INTRODUCTION

High levels of saturated fat consumption are correlated with increased risk of coronary heart disease. Traditional sunflower oil has about 130 g kg⁻¹ saturated fatty acid (SFA) content, which is considered low compared with most vegetable oils. However, canola oil is lower, with about 70 g kg⁻¹ SFA, and remains a major

* Corresponding author: Phone: +1 701 239 1322, Fax: +1 701 239 1346, e-mail: vickb@fargo.ars.usda.gov
competitor to sunflower oil in the marketplace. For sunflower oil to compete with canola oil and other vegetable oils with low SFA content, it is desirable to decrease its saturated fat concentration. To address this consumer preference, the USDA-ARS Sunflower Research Unit has recently released genetic stocks with reduced palmitic and stearic acids, the major SFAs of sunflower oil (Miller and Vick, 1999; Vick et al., 2003a).

Two genetic stocks, RS1 and RS2, were released in 2001 (Vick et al., 2003a). These stocks were derived from a cultivated sunflower line, PI 250542, collected in Egypt by Paul Knowles in 1958. RS1 has black seeds with gray stripes, while RS2 has light gray seeds that usually bleach to white in the sun. Both have a total SFA content (C16 to C24) of about 75 g kg⁻¹. In an earlier study (Vick et al., 2002) we reported on the inheritance of reduced SFA content in crosses of RS1 or RS2 with HA 821, which typically has a total SFA content of about 115 g kg⁻¹. However, after analysis of the inheritance data, we discovered that HA 821 was naturally low in palmitic acid, similar to RS1 and RS2, making it difficult to draw conclusions about the segregation of reduced palmitic acid in the progeny of crosses with RS1 or RS2. Therefore, we conducted a second inheritance study using inbred line HA 382 to cross with RS1 or RS2. HA 382 is a high yielding, high oil inbred line released in 1992 (Miller and Gulya, 1994), which has a palmitic, stearic, oleic, and linoleic acid content similar to commercial hybrids and other sunflower inbred lines.

In this study we report the results obtained from two years of field study on the inheritance of reduced palmitic and stearic acids in crosses between HA 382 and RS1 or RS2. A comparison of the data from the two years shows similarities in inheritance patterns between years, but also some variations, apparently caused by environmental differences. Preliminary results of this study were reported at annual meetings of the U.S. National Sunflower Association’s Sunflower Research Workshop (Vick et al., 2003b; Vick et al., 2004).

MATERIALS AND METHODS

Plant material. RS1 (PI 616494) and RS2 (PI 616495) were used as sources of reduced palmitic and stearic acids in crosses with HA 382 (PI 578871). HA 382 is an inbred line which has an SFA content (C16 to C24) of approximately 130 g kg⁻¹, that is typical of commercial sunflower. Seed was derived from reciprocal crosses of both RS1 and RS2 with HA 382. The F₁ seed of the four crosses [RS1/HA 382, HA 382/RS1, RS2/HA 382, and HA 382/RS2] was planted in the field in Fargo, ND, in 2002 and 2003, and the heads bagged for self-pollination to obtain F₂ seed. F₁ seed of the same four crosses was produced in the same field plot each year by emasculation and hand pollination. Heads of the parental lines, RS1, RS2, and HA 382, were bagged prior to flowering to obtain parental seed grown in the same environment as the F₁ and F₂ seed. The parental (N=50), F₁ (N=65-100), and F₂ (N=85-100) seed was harvested in September and was analyzed for fatty acid com-
position by gas chromatography. Seed was typically from one head, but in a few crosses with poor seed set, seed from as many as 13 heads was analyzed. Weather data, including sunflower growing degree days at the Fargo field plots, were obtained from the North Dakota Agricultural Weather Network (http://ndawn.ndsu.nodak.edu/application/sunflower-degree-days-form.html).

**Fatty acid composition analysis.** Parental, F₁, and F₂ seeds were cut in half and the distal end (not containing the embryo) was placed in a 1.5-ml gas chromatograph autosampler vial. After crushing the half seed with a blunt instrument, 1.5 ml of a solution of hexane-chloroform-0.5 mol dm⁻³ sodium methoxide in methanol (75:20:5, v/v) (sodium methoxide solution purchased from Sigma, St. Louis, MO**) was added to the vial and the vial capped. The sample was injected into a Hewlett-Packard 5890 gas chromatograph containing a DB-23 capillary column (30 m × 0.25 mm, J&W Scientific), which was held at 190°C for 5 min, then increased to 220°C at 10°C/min, held at 220°C for 1 min, then increased to 240°C at 20°C/min, and finally held at 240°C for 1.5 min, for a total run time of 11.5 min. Fatty acid concentrations are expressed as percent by weight of the total fatty acids. The total SFA composition is expressed as weight of the C16 to C24 SFAs per kg of all fatty acids.

**RESULTS**

**Inheritance of the reduced SFA trait in RS1**

**Parental lines (RS1 and HA 382).** RS1 had significantly lower SFA content than HA 382 in the field experiments of both 2002 and 2003. RS1 had an average total SFA concentration of 73-74 g kg⁻¹ compared with 128-129 g kg⁻¹ for HA 382 (Table 1). However, the relative proportions of palmitic and stearic acid changed between years. For RS1, the palmitic acid concentration was higher in 2003 (45 g kg⁻¹) compared with 2002 (39 g kg⁻¹). Conversely, the stearic acid concentration was lower in 2003 (20 g kg⁻¹) than in 2002 (26 g kg⁻¹). Thus, the total concentration of SFA remained about the same for both years. For HA 382, the concentrations of both palmitic and stearic acids were relatively stable over years. The palmitic acid concentration was 63 g kg⁻¹ in 2003 compared with 69 g kg⁻¹ in 2002, while the stearic acid concentration was 50 g kg⁻¹ in 2003 and 46 g kg⁻¹ in 2002.

**F₁ seed.** The F₁ seed from the reciprocal crosses of RS1 and HA 382 was intermediate between the parents for palmitic acid content in both 2002 and 2003 (Figures 1B, B’ and 1C, C’). The cross RS1/HA 382 produced a similar distribution of palmitic and stearic acids in both years. However, in the reciprocal cross, HA 382/RS1, there was an apparent environmental effect on palmitic acid concentration. In this cross there was a shift from 45 g kg⁻¹ palmitic acid in 2002 to 57 g kg⁻¹ in 2003.

**Names of products are included for the benefit of the reader and do not imply endorsement or preferential treatment by the United States Department of Agriculture.**
Table 1: Two-year study (2002 and 2003) on the fatty acid composition in the seed oil of RS1, HA 382, and the F1 and F2 progeny of reciprocal crosses of RS1 and HA 382

<table>
<thead>
<tr>
<th>Sample</th>
<th>Year</th>
<th>Palmitic 16:0</th>
<th>Stearic 18:0</th>
<th>Oleic 18:1</th>
<th>Linoleic 18:2</th>
<th>Arachidic 20:0</th>
<th>Gondoic 20:1</th>
<th>Béhenic 22:0</th>
<th>Lignoceric 24:0</th>
<th>Total g kg⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>RS1†</td>
<td>2002</td>
<td>39±2</td>
<td>26±3</td>
<td>401±36</td>
<td>518±39</td>
<td>2.0±0.2</td>
<td>2.1±0.1</td>
<td>5.9±2.7</td>
<td>1.9±0.3</td>
<td>74±4</td>
</tr>
<tr>
<td>RS1†</td>
<td>2003</td>
<td>45±2</td>
<td>20±3</td>
<td>317±29</td>
<td>596±30</td>
<td>1.9±0.9</td>
<td>2.0±0.1</td>
<td>5.0±1.0</td>
<td>1.8±0.5</td>
<td>73±5</td>
</tr>
<tr>
<td>HA 382†</td>
<td>2002</td>
<td>63±4</td>
<td>46±8</td>
<td>234±30</td>
<td>626±35</td>
<td>3.6±0.5</td>
<td>1.7±0.1</td>
<td>7.0±1.3</td>
<td>1.8±0.8</td>
<td>128±8</td>
</tr>
<tr>
<td>HA 382†</td>
<td>2003</td>
<td>63±6</td>
<td>50±8</td>
<td>223±35</td>
<td>635±33</td>
<td>3.6±0.6</td>
<td>1.8±0.1</td>
<td>8.8±1.4</td>
<td>3.3±0.6</td>
<td>129±10</td>
</tr>
<tr>
<td>RS1/HA 382 (F1)†</td>
<td>2002</td>
<td>49±3</td>
<td>26±3</td>
<td>341±39</td>
<td>559±39</td>
<td>2.2±0.3</td>
<td>2.2±0.5</td>
<td>7.0±1.1</td>
<td>2.4±0.4</td>
<td>87±4</td>
</tr>
<tr>
<td>RS1/HA 382 (F1)‡</td>
<td>2003</td>
<td>51±4</td>
<td>24±3</td>
<td>303±39</td>
<td>600±36</td>
<td>2.3±0.3</td>
<td>2.1±0.2</td>
<td>6.5±0.8</td>
<td>2.7±0.4</td>
<td>86±11</td>
</tr>
<tr>
<td>HA 382/RS1 (F1)†</td>
<td>2002</td>
<td>45±2</td>
<td>47±5</td>
<td>489±28</td>
<td>397±29</td>
<td>3.7±0.4</td>
<td>2.0±0.1</td>
<td>9.5±1.0</td>
<td>2.8±0.4</td>
<td>108±6</td>
</tr>
<tr>
<td>HA 382/RS1 (F1)‡</td>
<td>2003</td>
<td>57±5</td>
<td>44±7</td>
<td>290±32</td>
<td>585±31</td>
<td>3.6±0.6</td>
<td>1.8±0.2</td>
<td>8.2±1.5</td>
<td>2.8±0.7</td>
<td>113±6</td>
</tr>
<tr>
<td>RS1/HA 382 (F2)†</td>
<td>2002</td>
<td>50±3</td>
<td>33±6</td>
<td>382±37</td>
<td>518±37</td>
<td>2.6±0.4</td>
<td>1.9±0.2</td>
<td>7.2±1.0</td>
<td>1.4±0.5</td>
<td>95±7</td>
</tr>
<tr>
<td>RS1/HA 382 (F2)‡</td>
<td>2003</td>
<td>56±4</td>
<td>36±8</td>
<td>232±27</td>
<td>648±24</td>
<td>2.7±0.5</td>
<td>1.8±0.2</td>
<td>6.9±0.9</td>
<td>2.2±0.3</td>
<td>104±10</td>
</tr>
<tr>
<td>HA 382/RS1 (F2)†</td>
<td>2002</td>
<td>45±3</td>
<td>36±6</td>
<td>373±48</td>
<td>525±49</td>
<td>2.6±0.4</td>
<td>2.0±0.2</td>
<td>8.4±1.2</td>
<td>2.3±0.9</td>
<td>94±12</td>
</tr>
<tr>
<td>HA 382/RS1 (F2)‡</td>
<td>2003</td>
<td>60±4</td>
<td>26±7</td>
<td>275±27</td>
<td>616±27</td>
<td>2.4±0.6</td>
<td>2.0±0.2</td>
<td>6.5±1.4</td>
<td>2.3±0.7</td>
<td>97±9</td>
</tr>
</tbody>
</table>

† N=50, § N=100
Figure 1: Frequency distribution of palmitic acid in the parents (A, A'), F₁ (B, B', C, C'), and F₂ (D, D', E, E') progeny of the reciprocal crosses between RS1 and HA 382 grown in the field in 2002 and 2003.
(Table 1; and compare Figures 1C and 1C'). In addition, there appeared to be a maternal effect on total SFA content of the F1 seed. During both 2002 and 2003, the cross HA 382/RS1 produced F1 seed with 21 to 27 g kg⁻¹ higher SFA content than the RS1/HA 382 cross. The maternal effect was largely due to the consistently lower stearic acid in the RS1/HA 382 cross (Figures 2G, G' and 2H, H').

**F2 seed.** In both 2002 and 2003, the F2 seed of both crosses was intermediate in total SFA content, compared with the parents (Table 1). However, the palmitic acid concentration tended to be higher in 2003 than 2002, especially in the HA 382/RS1 cross (Table 1; Figure 1E, E'), suggesting that palmitic acid synthesis in this cross is influenced by environment more than in its reciprocal cross. The effect on total SFA in the HA 382/RS1 cross was tempered by a corresponding reduction in stearic acid content during the 2003 growing season (Table 1; Figure 2J, J'), so that the total SFA composition was similar in both years.

The palmitic acid content of the F2 seed did not segregate over the range of the palmitic acid content of the two parents (Figures 1D, D' and 1E, E'). Instead, the F2 seed had a somewhat narrow range of intermediate palmitic acid content. The stearic acid content of the F2 seed segregated more broadly than did palmitic acid, and the maternal influence observed in the F1 seed was less obvious in the F2 generation (Figures 2I, I' and 2J, J'). For the RS1/HA 382 cross, the mean was intermediate between the parents in both years; however, the reciprocal cross HA 382/RS1 showed a reduced stearic acid content in 2003. This was probably an environmental effect, because the reduced stearic acid was not observed in the F2 seed of this cross in 2002.

**Inheritance of the reduced SFA trait in RS2**

**Parental lines (RS2 and HA 382).** In both 2002 and 2003, RS2 was significantly lower in SFA content than HA 382. The average total SFA content of RS2 was 80-88 g kg⁻¹ compared with 127-129 g kg⁻¹ for HA 382 (Table 2). Both of the predominant SFA, palmitic and stearic, were lower in RS2 than in HA 382. But unlike RS1, the proportion of palmitic acid in RS2 did not increase in 2003; however, the concentration of stearic acid in RS2 decreased in 2003. Thus, the total concentration of SFA was slightly less in 2003, largely due to the lower stearic acid content. For HA 382, the concentrations of palmitic and stearic acids were similar between the years. The palmitic acid concentration was 63 g kg⁻¹ in 2003 compared with 69 g kg⁻¹ in 2002, while the stearic acid concentration was 50 g kg⁻¹ in 2003 and 46 g kg⁻¹ in 2002.

**F1 seed.** In both 2002 and 2003, the total SFA content in the F1 seed (85 and 102 g kg⁻¹, respectively) of the RS2 by HA 382 cross was intermediate between the parents, RS2 (80-88 g kg⁻¹) and HA 382 (127-129 g kg⁻¹) (Table 2). The reciprocal cross HA 382/RS2 produced F1 seed with 106-112 g kg⁻¹ total SFA, also intermediate between RS2 and HA 382.
Table 2: Two-year study (2002 and 2003) on the fatty acid composition in the seed oil of RS2, HA 382, and the F1 and F2 progeny of reciprocal crosses of RS2 and HA 382

<table>
<thead>
<tr>
<th>Sample</th>
<th>Year</th>
<th>Palmitic 16:0 g kg⁻¹</th>
<th>Stearic 18:0 g kg⁻¹</th>
<th>Oleic 18:1 g kg⁻¹</th>
<th>Linoleic 18:2 g kg⁻¹</th>
<th>Arachid 20:0 g kg⁻¹</th>
<th>Gondoic 20:1 g kg⁻¹</th>
<th>Behenic 22:0 g kg⁻¹</th>
<th>Lignoceric 24:0 g kg⁻¹</th>
<th>Total Satd FA g kg⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>RS2 †</td>
<td>2002</td>
<td>45±3</td>
<td>32±5</td>
<td>429±56</td>
<td>477±58</td>
<td>2.4±0.2</td>
<td>1.8±0.1</td>
<td>7.3±0.7</td>
<td>1.8±0.2</td>
<td>88±6</td>
</tr>
<tr>
<td>RS2 ‡</td>
<td>2003</td>
<td>44±4</td>
<td>26±4</td>
<td>340±69</td>
<td>560±59</td>
<td>2.1±0.4</td>
<td>1.8±0.2</td>
<td>6.3±1.2</td>
<td>2.0±0.4</td>
<td>80±7</td>
</tr>
<tr>
<td>HA 382†</td>
<td>2002</td>
<td>69±4</td>
<td>46±8</td>
<td>234±30</td>
<td>626±34</td>
<td>3.6±0.5</td>
<td>1.7±0.1</td>
<td>7.0±1.3</td>
<td>1.8±0.8</td>
<td>127±8</td>
</tr>
<tr>
<td>HA 382†</td>
<td>2003</td>
<td>63±6</td>
<td>50±8</td>
<td>223±35</td>
<td>635±33</td>
<td>4.1±0.6</td>
<td>1.8±0.1</td>
<td>8.8±1.4</td>
<td>3.3±0.6</td>
<td>129±10</td>
</tr>
<tr>
<td>RS2/HA 382 (F1)†</td>
<td>2002</td>
<td>45±3</td>
<td>29±3</td>
<td>437±43</td>
<td>468±43</td>
<td>2.2±0.2</td>
<td>1.9±0.1</td>
<td>6.5±0.9</td>
<td>1.8±0.3</td>
<td>85±3</td>
</tr>
<tr>
<td>RS2/HA 382 (F1)§</td>
<td>2003</td>
<td>62±6</td>
<td>29±4</td>
<td>285±36</td>
<td>602±33</td>
<td>2.5±0.4</td>
<td>1.8±0.2</td>
<td>5.9±1.0</td>
<td>2.4±0.5</td>
<td>102±9</td>
</tr>
<tr>
<td>HA 382/RS2 (F1)†</td>
<td>2002</td>
<td>46±2</td>
<td>44±5</td>
<td>474±26</td>
<td>415±28</td>
<td>3.6±0.3</td>
<td>2.0±0.1</td>
<td>9.8±0.8</td>
<td>3.0±0.3</td>
<td>106±7</td>
</tr>
<tr>
<td>HA 382/RS2 (F1)‡</td>
<td>2003</td>
<td>55±6</td>
<td>42±7</td>
<td>270±35</td>
<td>606±31</td>
<td>3.5±0.6</td>
<td>1.9±0.8</td>
<td>8.7±1.5</td>
<td>3.3±0.6</td>
<td>112±12</td>
</tr>
<tr>
<td>RS2/HA 382 (F2)‡</td>
<td>2002</td>
<td>47±5</td>
<td>45±8</td>
<td>450±72</td>
<td>439±73</td>
<td>3.3±0.5</td>
<td>1.8±0.1</td>
<td>9.1±1.5</td>
<td>1.5±0.5</td>
<td>105±9</td>
</tr>
<tr>
<td>RS2/HA 382 (F2)†</td>
<td>2003</td>
<td>56±5</td>
<td>34±8</td>
<td>339±51</td>
<td>550±53</td>
<td>2.6±0.5</td>
<td>1.9±0.2</td>
<td>7.4±1.3</td>
<td>1.8±0.5</td>
<td>102±9</td>
</tr>
<tr>
<td>HA 382/RS2 (F2)†</td>
<td>2002</td>
<td>49±3</td>
<td>43±7</td>
<td>410±42</td>
<td>478±43</td>
<td>3.3±0.5</td>
<td>1.9±0.8</td>
<td>9.6±1.5</td>
<td>2.4±0.4</td>
<td>107±8</td>
</tr>
<tr>
<td>HA 382/RS2 (F2)‡</td>
<td>2003</td>
<td>50±4</td>
<td>37±6</td>
<td>370±59</td>
<td>519±59</td>
<td>3.0±0.7</td>
<td>1.9±0.2</td>
<td>7.9±1.3</td>
<td>2.2±0.5</td>
<td>100±2</td>
</tr>
</tbody>
</table>

† N=50
‡ N=100
§ N=65
* N=85
Figure 2: Frequency distribution of stearic acid in the parents (F, F'), F₁ (G, G', H, H'), and F₂ (I, I', J, J') progeny of the reciprocal crosses between RS1 and HA 382 grown in the field in 2002 and 2003.
The distribution of palmitic and stearic acids in the F1 seed from the reciprocal crosses of RS2 and HA 382 in the field in 2003 was different than that observed in 2002, suggesting that environment affected SFA synthesis. Whereas in 2002, the reciprocal crosses between RS2 and HA 382 both resulted in low palmitic acid phenotypes, in 2003 the palmitic acid concentration in the F1 seed of the reciprocal crosses was increased. In 2003, the RS2/HA 382 cross had a higher palmitic acid content, similar to HA 382 (Table 2, Figure 3B'), while the reciprocal cross had a palmitic acid content intermediate between the two parents (Figure 3C').

The distribution of stearic acid was similar for both years (Figures 4G, G' and 4H, H'), with an apparent maternal effect for both crosses. As in 2002, the RS2/HA 382 cross resulted in a reduced stearic acid content similar to the RS2 female parent, whereas the reciprocal cross HA 382/RS2 was intermediate between the parents.

**F2 seed.** In both 2002 and 2003, the F2 seed of both crosses was intermediate in total SFA content compared with the parents (Table 2). The palmitic acid concentration tended to be higher in 2003 (Figures D', E') than in 2002 (Figures 3D, E), an effect that was also observed in the F2 seed of reciprocal crosses of RS1 with HA 382 (compare Figures 1D', E' with Figures 1D, E). However, the total SFA content was similar in both years because the increased palmitic acid in 2003 was balanced by a corresponding reduction in stearic acid content during the 2003 growing season.

The palmitic acid content of the F2 seed did not segregate over the range of the parents (Figures 3D, D' and 3E, E'). Instead, the F2 seed had a somewhat narrow range of intermediate palmitic acid content. The stearic acid content of the F2 seed segregated more broadly than did palmitic acid (Figures 4I, I' and 4J, J'), and the maternal influence observed in the F1 seed was less pronounced in the F2 generation. The mean stearic acid concentration was intermediate between the parents. We did not observe the apparent environmental effect of reduced stearic acid in the F2 seed of HA 382/RS2 that was observed in the HA 382/RS1 cross (compare Figure 4J' with Figure 2J').

**DISCUSSION**

The inheritance of SFA content has been studied in a number of mutant sunflower and soybean lines in which the SFA composition has been altered. Erickson et al. (1988) and Fehr et al. (1991) each developed a mutant soybean line in which the palmitic acid content was reduced from about 100-120 g kg⁻¹, typical for commercial cultivars, to about 70 g kg⁻¹. The F2 plants of a cross between these two low-palmitic soybean lines segregated to produce some progeny that were further reduced in palmitic acid content to about 44 g kg⁻¹, indicating that two alleles at independent loci, acting additively, were responsible for the low-palmitic trait. Sim-
Figure 3: Frequency distribution of palmitic acid in the parents (A, A'), F₁ (B, B', C, C'), and F₂ (D, D', E, E') progeny of the reciprocal crosses between RS2 and HA 382 grown in the field in 2002 and 2003.
Figure 4: Frequency distribution of stearic acid in the parents (F, F'), F₁ (G, G', H, H'), and F₂ (I, I', J, J') progeny of the reciprocal crosses between RS2 and HA 382 grown in the field in 2002 and 2003.
ilar results were reported by Primomo et al. (2002) for two new low-palmitic germ-
plasm lines, RG3 and RG1.

Miller and Vick (1999) generated three sunflower mutant lines that were
reduced in total SFAs. One mutant line was reduced in palmitic acid, and the other
two mutant lines were reduced in stearic acid. Inheritance studies showed that the
low-palmitic acid content was controlled by a single gene with additive gene action.
The low-stearic acid content was controlled by a single gene in one mutant, and by
two genes in the other mutant, both with additive gene action.

Inheritance studies have also been reported for several sunflower mutants with
high saturated fatty acid content. Two high-palmitic acid sunflower mutants, CAS-5
and CAS-12, each with palmitic acid content greater than 250 g kg\(^{-1}\), were
described by Pérez-Vich et al. (1999a, 2002a). The high palmitic acid content of
CAS-5 was concluded to result from the presence of a mutant recessive allele, \(p1\),
and one of two other recessive alleles, \(p2\) or \(p3\), already present in the line prior to
mutation. The inheritance of high palmitic acid in CAS-12 was similar, being con-
trolled by the partially recessive alleles, \(p1\), \(p2\), and \(p3\). Similarly, the genetic con-
trol of a high-stearic acid (about 250 g kg\(^{-1}\)) sunflower mutant, CAS-3, has been
investigated (Pérez-Vich et al., 1999b). Two recessive genes, \(es1\) and \(es2\), at two
independent loci were proposed to be responsible for the high-stearic acid trait of
CAS-3, having the genotype \(es1es1es2es2\). In another sunflower mutant, CAS-4
(medium-stearic), the stearic acid content (about 130 g kg\(^{-1}\)), was found to be con-
trolled by the same \(es2\) gene and a second gene, different from \(es1\), termed \(es1b\)
(Pérez-Vich et al., 2002b). The genotype of CAS-4 was proposed to be
\(es1bes1bes2es2\).

In a practical sense, the expression of the reduced palmitic and stearic acid
traits is most important in the \(F_2\) seed, which is harvested commercially and
crushed for oil. The \(F_2\) generation is also important for plant breeders because it is
the segregating generation where selections can be made by companies using RS1
and RS2 to lower the SFA content of their parental lines. Our experiments showed
that the inheritance and expression of the reduced palmitic and stearic acid con-
tents of RS1 and RS2 are complex and apparently multigenic. The greatest reduc-
tion (~25%) in SFAs in the \(F_2\) seed was achieved when RS1 was a parent.

The relative changes in palmitic and stearic acid contents between the two
-growing seasons suggest that environmental conditions play a significant role in the
proportions of palmitic and stearic acids. While we do not know the specific envi-
ronmental parameter(s) responsible for the altered proportions of palmitic and
stearic acids, temperature may have contributed to the differences between years.
Figure 5 shows thermal availability (daily sunflower growing degree days) during
the seed development period in 2002 and 2003. The weather data for the field plots
showed that there was a substantial difference in timing of heat input between
years. In 2002, the period of early seed development (~August 15-21) was cool, fol-
lowed by a warmer period (August 22 - September 8). In 2003, the temperature
trend during seed development was reversed, with a warm early period (~August 15-21) and cooler later (August 22 - September 8). Linoleic acid content increases with cooler temperatures, and our data show a significantly higher linoleic acid concentration in the seed harvested in 2003 (Tables 1 and 2). Therefore, it may be that differences in fatty acid composition of the seeds were largely determined by temperature during the active seed filling period from August 22 to September 8, when temperatures were cooler in 2003 than in 2002. The total SFA content was also influenced by environment, having opposite effects with RS1 (higher total SFA in 2003) and RS2 (lower total SFA in 2003).

**CONCLUSIONS**

The reduced SFA phenotype in the F₂ generation is largely due to inheritance of the trait from RS1 and RS2. Environment also plays a role in achieving reduced content of SFA. Thus, it can be expected that the level of SFAs in cultivated hybrid sunflower with genes from RS1 or RS2 in one of the parents will vary from year to year. Therefore, to achieve the lowest possible concentration of SFAs in the F₂ seed, it will be necessary to incorporate the reduced SFA trait into both parents of a hybrid.

**ACKNOWLEDGMENTS**

*The skilled technical assistance of Lisa Brown and Leonard Cook is gratefully acknowledged.*
REFERENCES


Miller, J.F. and Gula, T.J., 1994. Registration of four maintainer (HA 382 to HA 385) and four restorer (RHA 386 to RHA 389) sunflower germplasm lines. Crop Sci. 34: 286.


ESTUDIO BIANUAL DE HERENCIA DEL CONTENIDO REDUCIDO DE ÁCIDOS GRASOS SATURADOS EN LA SEMILLA DE GIRASOL

RESUMEN

RS1 y RS2 son dos bases genéticas que contienen bajo contenido de ácidos grasos saturados. Aquí hacemos la relación de los resultados de bienio sobre la herencia de los ácidos palmitico y esteárico en RS1 y RS2, en la generación de cruzamiento F1 y F2 con HA 382, la línea consanguínea (inbred), cuyo contenido de ácidos grasos es semejante a muchos híbridos comerciales de girasol. La expresión del contenido reducido de los ácidos palmitico y esteárico es la más importante en la generación F2 porque la semilla F2 es la que el granjero siega y vende y de la cual se produce aceite. Nuestros ensayos han demostrado que la semilla F2 de los cruzamientos recíprocos de RS1 ó RS2 con HA 382 era intermediaria en el contenido de los aceites grasos saturados entre dos progenitores híbridos. La herencia y la expresión de los ácidos palmitico y esteárico reducidos en RS1 y RS2 eran bajo control de más de un gen. Además, los cambios relativos significantes en contenido de los ácidos palmitico y esteárico entre los periodos vegetativos en los años 2002 y 2003, indican que el entorno tenía un papel importante en las relaciones relativas...
entre los ácidos grasos. También, el total contenido de los ácidos grasos era bajo la influencia del entorno, generando efectos contradictorios en RS1 (incrementado el total contenido de ácidos grasos en el año 2003) y RS2 (reducido el total contenido de ácidos grasos en el año 2003). Esos datos indican que es necesario introducir el reducido contenido de ácidos grasos en ambos progenitores del híbrido, para lograr la más baja concentración de los ácidos grasos saturados en la semilla F₂.

ÉTUDE DE DEUX ANS PORTANT SUR LA TRANSMISSION DU CONTENU RÉDUIT D’ACIDES GRAS SATURÉS DANS LA GRAINE DE TOURNESOL

RÉSUMÉ

RS1 et RS2 sont deux bases génétiques qui possèdent un faible contenu d’acides gras saturés. Nous faisons part ici des résultats d’une étude de deux ans sur la transmission des acides palmitique et stéarique de RS1 et RS2 dans les générations du croisement F₁ et F₂ avec HA 382, une lignée ayant une composition d’acides gras semblable à celle de plusieurs hybrides de tournesol commerciaux. L’expression du contenu réduit d’acides palmitique et stéarique est la plus importante dans la génération F₂ parce que c’est celle qui est cultivée par les fermiers, vendue et pressée pour l’extraction d’huile. Nos expériences ont démontré que la graine F₂ des croisements réciproques de RS1 ou RS avec HA 382 était intermédiaire pour le contenu d’acides gras saturés entre les deux parents hybrides. La transmission et l’expression des caractéristiques palmitique et stéarique de RS1 et RS2 ont été contrôlées par plus d’un gène. De plus, des changements relatifs importants dans les contenus d’acide palmitique et stéarique entre les saisons de végétation de 2002 et 2003 donnent à penser que l’environnement a un rôle important dans les proportions relatives de ces acides gras. Le contenu total d’acides gras saturés a aussi été influencé par l’environnement, produisant des effets opposés avec RS1 (total d’acides gras saturés augmenté en 2003) et RS2 (total d’acides gras saturés diminué en 2003). Ces données démontrent qu’il est nécessaire d’incorporer la caractéristique d’acides gras saturés réduite dans les deux parents d’un hybride de manière à obtenir la plus basse concentration d’acides gras saturés dans la graine F₂.