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# Effect of Perfluidone on Metabolism of Lipids in Maize (*Zea mays* L.) and Sunflower (*Helianthus annuus* L.)

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**Abstract.** Treatment of germinating maize seedlings with 0.126 mM of the herbicide Perfluidone (Destun) (1,1,1-trifluoro-4′-[phenylsulfonyl]-methanesulfona-*o*-toluidide) for 2 days in the dark, then 3 days in the light, at 25°C causes decreases in fresh weight, dry weight, shoot length, and in total chlorophyll and carotenoid contents; in contrast, sunflower seedlings seem not to be affected. Perfluidone causes marked decreases in total lipids and in glyco- and phospholipids of maize seedlings. In sunflower cotyledons, total lipids and pigments (chlorophyll, carotenoids) are not affected, but there is an increase in glycolipids at the expense of phospholipids. After Perfluidone treatment, a significant increase in the fatty acid mole ratio (18:0 + 18:1 + 18:2)/18:3 was found for the maize glycolipids, monogalactosyl diacylglycerol (MGD), digalactosyl diacylglycerol (DGD), and sterol glycoside (SG) + esterified sterol glycoside (ESG), and for the phospholipid, phosphatidylcholine (PC). In sunflower seedlings, however, only the fatty acid mole ratio of ESG + SG showed an increase and that of phosphatidylserine (PS) showed a large decrease. The differential response of the two plant species to Perfluidone suggests that the control of linolenic acid biosynthesis may vary depending on plant species and/or on plant tissues.

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**Abbreviations:** PG, phosphatidylglycerol; PC, phosphatidylcholine; PE, phosphatidylethanolamine; PI, phosphatidylinositol; PS, phosphatidylserine; MGD, monogalactosyl diacylglycerol DGD, digalactosyl diacylglycerol; SQD, sulfoquinovosyl diacylglycerol; SG, sterol glycoside ESG, esterified sterol glycoside; FA, fatty acid.

St. John and Hilton (1973) have shown that Perfluidone (Destun) (1,1,1-trifluoro-4'-[phenylsulfonyl]-methanesulfono-*o*-toluidide) inhibited enzyme synthesis of glycerides *in vitro*. Using intact wheat (*Triticum aestivum* L.), they demonstrated an inhibition of glyceride synthesis *in vivo* as evidenced by a build up in free fatty acids and a decrease in neutral and polar lipids. They suggested that Perfluidone alters membrane structure and function through an inhibition of membrane lipid synthesis. They did not isolate individual neutral lipids, phospholipids, or glycolipids, but showed that the reduction in total polar lipid levels results from substantial decreases in all of the component fatty acids of polar lipids, the largest decrease being in linolenic acid (18:3, 20% of control) and the smallest in oleic acid (18:1; 69% of control).

We therefore have investigated the effect of Perfluidone on lipids of a monocot (maize [*Zea mays* L.]) and a dicot (sunflower [*Helianthus annuus* L.]) and have examined changes in the individual polar and neutral lipid components as well as carotenoids and chlorophylls.

## Materials and Methods

### *Plants*

Maize (*Zea mays* L.) var. Sunnyvee seeds treated with Vitavax-T and sunflower (*Helianthus annuus* L.) var. Ontario seeds were provided by the Ontario Seed Co. Ltd., Waterloo, Ontario, Canada. The seeds were germinated in 9-cm Petri dishes on four layers of moist filter paper soaked in either 0.126 mM Perfluidone or in water (controls) for 2 days in the dark, followed by 3 days in the light (Westinghouse fluorescent tubes giving a light intensity of 4500 lx), at 25 ± 1°C. Preliminary studies have shown that 0.126 mM Perfluidone inhibited growth of the seedlings without actually killing them.

### *Lipid Analysis*

Five-day-old maize shoots and sunflower cotyledons were harvested and immediately frozen on dry ice. The tissues were quickly macerated and extracted three times with hot isopropanol in a mortar and pestle, and the dried extract was further extracted by the method of Bligh and Dyer (1959) (see Evans et al. 1982 and Kates 1972). The total lipids were estimated gravimetrically.

A known quantity of internal standard (17:0 acid) was added to an aliquot of the total lipid extract in chloroform, and the solvent was evaporated under a stream of nitrogen. The residual lipids were converted to fatty acid methyl esters by methanolysis in 2.5% methanolic-gaseous HCl (Kates 1972). Fatty acid methyl esters were analyzed by gas-liquid chromatography on a column (2 m × 0.4 cm) of 10% SP-2330 on 100/120 chromosorb WAW at 225°C. Peaks

were identified by comparison of retention times with those of authentic standards and quantitated by integration of peak areas (Ferrante et al. 1983).

*Chromatography*

*Neutral Lipids.* Another aliquot of the total lipid extract was used to obtain the neutral lipids by one-dimensional thin-layer chromatography (TLC) on silica gel G layers (0.25 mm thick) spread on 20 cm × 20 cm glass plates purchased from Brinkmann Co. The solvent system used was petroleum ether:diethyl ether:90% formic acid (40:10:1, v/v) (Christie 1973) in which the polar lipids stayed at the origin.

*Polar Lipids.* Two-dimensional thin-layer chromatography of lipids was performed on the same type of TLC plates used for neutral lipids in the solvent system: (first dimension) $CHCl_3$:MeOH:acetone:diethylamine:$H_2O$ (120:35:37.5:6:4.5, v/v) and (second dimension) $CHCl_3$:MeOH:conc. $NH_4OH$ (65:25:5, v/v) (Evans et al. 1982).

Lipids were detected using the following spray reagents: $(NH_4)_2$ $MoO_4$/$HClO_4$ for phosphatides; 0.5% α-naphthol/$H_2SO_4$ (w/v) for glycolipids; 0.25% ninhydrin in acetone/lutidine 9:1 (w/v) for primary amino-containing lipids; 50% $H_2SO_4$/50% ethanol (v/v) followed by charring for detection of all lipids (Kates 1972).

For quantitation, lipid spots visualized by spraying with Rhodamine 6G were scraped off the plate and methanolized by heating in 2.5% methanolic—HCl together with an internal standard (Kates 1972). Fatty acid methyl ester peaks were identified and quantitated as already described under lipid analysis.

*Determination of Chlorophyll.* An aliquot of the total lipid extract was partitioned into diethyl ether and absorbance was measured at 642.5 and at 660 nm. Chlorophyll content was calculated according to the equations of Comar and Zschiele (1942).

*Carotenoid Determination.* An aliquot of total lipid extract was saponified using 10% KOH in methanol (w/v) (Valadon and Mummery 1975). The unsaponifiable material was extracted with diethyl ether and washed free of alkali with distilled water; chlorophylls were removed by this treatment. The ether extract was taken to dryness and the residue dissolved in hexane. Procedures for the phase-partition of carotenoids between hexane and aqueous 90% (v/v) methanol and the separation and identification of carotenoids by column and by thin-layer chromatography were as described by Valadon and Mummery (1977).

The structural identity of individual carotenoids was established by comparison with authentic samples (Hoffmann, La Roche, Basle), using chromatographic methods as already described (Valadon and Mummery 1975, 1977).

The concentration of individual carotenoids was determined by measuring $E_{max}$ and comparing it with known $E^{1\%}_{1cm}$ (Valadon and Mummery, 1975). For those pigments whose $E^{1\%}_{1cm}$ values were unknown, $E_{max}$ was assumed to be 2500 (Valadon and Mummery, 1975). Total carotenoids were obtained by adding values for individual carotenoids together.

Each experiment was repeated twice in duplicate, so that the mean obtained was for four replicates with ± s.d. where appropriate. When not indicated, s.d. values are less than ± 10%.

## Results and Discussion

Perfluidone at the concentration used (0.126 mM) had very obvious effects on the maize seedlings. Fresh weight, dry weight, and shoot lengths were greatly decreased, as were also the chlorophyll and carotenoid contents (Table 1). The sunflower cotyledons, in contrast, did not show any obvious effects after Perfluidone treatment, as controls and treated seedlings had very similar dry weight, fresh weight, total chlorophyll, and total carotenoid values (Table 1). The difference between maize and sunflower may be due to the fact that the former is a mono- and the latter a dicotyledonous plant. The difference may also be caused by differential absorption, translocation, and/or metabolism of the herbicide; Perfluidone may also be changed or degraded more by sunflower tissue than by maize tissue.

Perfluidone caused marked alterations in certain maize lipid levels *in vivo* (Table 1). Whereas the content of neutral lipids per 100 shoots was affected somewhat, both glyco- and phospholipid contents were greatly reduced. The polar lipids, therefore, appear to be more affected by Perfluidone than the neutral (nonpolar) lipids. The reduction in polar lipid levels can also be seen on a shoot/dry weight basis (Table 1), the largest decreases being in PC, PG, and DGD. These results are of interest, since it is known that glycolipids and PG are predominantly associated with the chloroplast membranes of shoots, whereas phospholipids (PC, PE, PI) predominate in mitochondrial and microsomal membranes. Under our conditions of growth, there would thus be a greater volume of chloroplasts compared to mitochondria and endosplasmic reticulum, based on the higher total amount of glycolipids compared to phospholipids.

St. John (1982) has studied the effect of substituted pyridazinone herbicides on various plants and has suggested, in light of the differential responses (depending on the substitution), that control of linolenic acid biosynthesis may vary depending on plant species and even on the tissue. She used the mole ratio 18:2/18:3 as her criterion. In the present study, a better criterion for linolenic acid biosynthesis was found to be the mole ratio (18:0 + 18:1 + 18:2)/18:3. We found a significant increase in this ratio for the glycolipids MGD, DGD, and ESG + SG and for the phospholipid PC (Tables 2 and 3). No

. **Table 1.** Effect of Perfluidon on maize and sunflower lipids.

| | Maize | | | | Sunflower | | | |
|---|---|---|---|---|---|---|---|---|
| | Controls | | 0.126 mM Perfluidone | | Controls | | 0.126 mM Perfluidone | |
| | Per 100 shoots | % total lipids | Per 100 shoots | % total lipids | Per 100 shoots | % total lipids | Per 100 shoots | % total lipids |
| Fresh wt (g) | 24.4 ± 2.1 | — | 16.4 ± 1.2 | — | 16.4 ± 1.5 | — | 16.7 ± 1.4 | — |
| Dry wt (g) | 1.5 ± 0.1 | — | 1.0 ± 0.1 | — | 1.8 ± 0.1 | — | 1.9 ± 0.1 | — |
| Total Lipids (mg) | 141.1 ± 12.0 | 100.0 | 69.3 ± 6.2 | 100.0 | 267.6 ± 22.2 | 100.0 | 272.2 ± 24.5 | 100.0 |
| Sterol esters + sterols (mg) | 16.8 | 11.9 | 11.3 | 16.3 | 23.0 | 8.6 | 21.0 | 7.7 |
| FA + FA esters (mg) | 34.3 | 24.3 | 30.4 | 43.9 | 15.4 | 5.8 | 15.8 | 5.8 |
| Triglycerides (mg) | — | — | — | — | 50.8 | 19.0 | 51.2 | 18.8 |
| Unknown (mg) | — | — | — | — | 8.4 | 3.1 | 8.0 | 2.9 |
| Diglycerides (mg) | 14.1 | 10.0 | 3.2 | 4.6 | 30.8 | 11.5 | 29.8 | 10.9 |
| Monoglycerides (mg) | 11.1 | 7.9 | 8.7 | 12.6 | 13.4 | 5.0 | 14.6 | 5.4 |
| Total Neutral Lipids (mg) | 76.3 ± 6.5 | 54.1 | 53.6 ± 4.5 | 77.4 | 141.8 ± 11.8 | 53.0 | 140.4 ± 12.6 | 51.5 |
| PG (mg) | 7.3 | 5.2 | 0.7 | 1.0 | 26.6 | 9.9 | 15.4 | 5.7 |
| PC (mg) | 5.1 | 3.6 | 0.5 | 0.7 | 13.2 | 4.9 | 5.2 | 1.9 |
| PE (mg) | 1.1 | 0.8 | 0.5 | 0.7 | 2.8 | 1.0 | 2.8 | 1.0 |
| PI (mg) | 1.0 | 0.7 | 0.5 | 0.7 | 2.0 | 0.7 | 2.4 | 0.9 |
| PS (mg) | 1.2 | 0.9 | 1.1 | 1.6 | 2.4 | 0.9 | 2.2 | 0.8 |
| Total Phospholipids (mg) | 15.7 ± 1.3 | 11.2 | 3.3 ± 0.3 | 4.7 | 47.0 ± 4.0 | 17.4 | 28.0 ± 2.2 | 10.3 |
| MGD (mg) | 12.4 | 8.8 | 4.2 | 6.1 | 42.0 | 15.7 | 43.0 | 15.8 |
| DGD (mg) | 18.5 | 13.1 | 2.6 | 3.8 | 14.6 | 5.5 | 25.6 | 9.4 |
| SQD (mg) | 9.8 | 6.9 | 2.1 | 3.0 | 9.6 | 3.6 | 25.0 | 9.2 |
| Cerebrosides (mg) | 6.9 | 4.9 | 2.4 | 3.5 | 9.4 | 3.5 | 7.4 | 2.7 |
| ESG + SG (mg) | 1.5 | 1.0 | 1.1 | 1.5 | 3.2 | 1.3 | 2.8 | 1.1 |
| Total Glycolipids (mg) | 49.1 ± 4.2 | 34.7 | 12.4 ± 1.1 | 17.9 | 78.8 ± 6.5 | 29.6 | 103.8 ± 9.3 | 38.2 |
| Total Complex Lipids (mg) | 64.8 ± 5.5 | 45.9 | 15.7 ± 1.4 | 22.6 | 125.8 ± 10.5 | 47.0 | 131.8 ± 12.0 | 48.5 |
| Total Chlorophylls (mg) | 109.0 ± 9.7 | — | 45.9 ± 4.4 | — | 312.2 ± 25.5 | — | 306.7 ± 28.6 | — |
| Total Carotenoids (μg) | 28.4 ± 2.6 | — | 9.2 ± 0.8 | — | 84.2 ± 7.8 | — | 84.8 ± 7.8 | — |
| Shoot length (cm/seedling) | 7.5 ± 0.6 | — | 3.8 ± 0.3 | — | 4.4 ± 0.3 | — | 4.0 ± 0.4 | — |

**Table 2.** Effect of 0.126 mM Perfluidone on fatty acid composition of glycolipids in maize and in sunflower. The results are expressed as mole % of total fatty acids.

| | | 16:0 | 16:1 | 18:0 | 18:1 | 18:2 | 18:3 | 20:0–22:0[b] | 18:2/18:3 | 18:0 + 1 + 2/18:3 |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | *MDG* | | | | |
| Maize | (Con)[a] | 7.5 | 2.1 | 1.1 | 10.1 | 23.8 | 52.5 | 2.9 | 0.45 | 0.67 |
| | (Herb) | 10.9 | 4.3 | 8.5 | 14.8 | 27.2 | 30.6 | 3.7 | 0.88 | 1.65 |
| Sunfl | (Con) | 10.3 | 1.3 | 8.2 | 11.2 | 12.8 | 52.5 | 3.7 | 0.24 | 0.61 |
| | (Herb) | 10.6 | 1.6 | 7.2 | 15.6 | 13.5 | 50.9 | 0.6 | 0.26 | 0.71 |
| | | | | | | *DGD* | | | | |
| Maize | (Con) | 21.9 | 1.4 | 4.1 | 11.3 | 17.2 | 41.9 | 2.2 | 0.41 | 0.77 |
| | (Herb) | 18.3 | 1.2 | 3.5 | 9.4 | 44.1 | 21.8 | 1.7 | 2.02 | 2.61 |
| Sunfl | (Con) | 14.8 | 1.4 | 7.8 | 3.7 | 30.2 | 40.2 | 1.9 | 0.75 | 1.03 |
| | (Herb) | 17.4 | — | 9.9 | 4.7 | 24.1 | 38.7 | 5.2 | 0.62 | 1.00 |
| | | | | | | *SQD* | | | | |
| Maize | (Con) | 13.2 | 0.8 | 3.6 | 5.8 | 48.2 | 24.8 | 3.6 | 1.94 | 2.32 |
| | (Herb) | 18.4 | 2.4 | 6.7 | 10.3 | 40.5 | 19.0 | 2.7 | 2.13 | 3.02 |
| Sunfl | (Con) | 13.3 | 3.3 | 6.5 | 11.6 | 52.8 | 11.8 | 0.7 | 4.47 | 6.01 |
| | (Herb) | 14.8 | 1.8 | 6.2 | 9.9 | 51.5 | 10.5 | 5.3 | 4.90 | 6.43 |
| | | | | | | *Cerebrosides* | | | | |
| Maize | (Con) | 27.8 | 0.6 | 11.5 | 8.9 | 33.7 | 13.3 | 4.2 | 2.53 | 4.06 |
| | (Herb) | 29.8 | 1.2 | 3.2 | 6.2 | 45.6 | 11.3 | 2.7 | 4.04 | 4.86 |
| Sunfl | (Con) | 19.2 | 1.4 | 5.9 | 6.0 | 44.2 | 22.2 | 1.1 | 1.99 | 2.52 |
| | (Herb) | 21.4 | 2.9 | 6.3 | 6.8 | 36.9 | 21.8 | 3.9 | 1.69 | 2.29 |
| | | | | | | *ESG + SG* | | | | |
| Maize | (Con) | 21.9 | — | 6.7 | 12.6 | 35.6 | 12.8 | 11.9 | 2.78 | 4.28 |
| | (Herb) | 29.3 | — | 7.5 | 14.4 | 42.9 | 4.3 | 1.6 | 9.97 | 15.07 |
| Sunfl | (Con) | 12.1 | 3.7 | 9.1 | 14.0 | 38.0 | 8.8 | 14.3 | 4.31 | 6.94 |
| | (Herb) | 19.4 | — | 11.4 | 31.6 | 31.0 | 2.2 | 5.4 | 14.09 | 33.60 |

[a] Con = control; Herb = herbicide; Sunfl = sunflower.
[b] Includes 20:0, 20:1, 20:3, 20:4, and 22:0.

signficant changes in the ratio for any of the major neutral lipids (FA + FA methyl esters, triglycerides, diglycerides) were found (Table 4).

Pyrazon, one of the pyridazinones, affected neither chlorophyll nor carotenoid accumulation nor fatty acid composition of either MGD or DGD. On the other hand, San 9774 (the trifluoride substitute of pyrazon) preferentially affected the fatty acid composition of MGD compared to DGD (St. John 1982). In our studies with maize, however, Perfluidone, while affecting the fatty acid composition of both MGD and DGD, appeared to cause a greater decrease in 18:3 and a greater increase in 18:2 in DGD than in MGD (Table 2, see ratios 18:2/18:3 and 18:0 + 1 + 2/18:3). The content of DGD (on a fresh-shoot or dry-wt basis) is also reduced to a greater extent than is MGD (Table 1), and the content of chlorophylls and carotenoids were also greatly reduced.

Plant species differ in their susceptibility to herbicides. In the present study, maize was found to be more sensitive than sunflower, which, at first glance, seemed not to be affected at all. However, even though fresh weight, dry weight, and content of carotenoids, chlorophylls, and total lipids of sunflower cotyledons were not affected, there was an obvious effect on the polar lipids: an increase in glycolipids at the expense of phospholipids (Table 1). Individually, there was an increase in contents of DGD and SQD and a decrease in PG and PC. ESG + SG showed the largest increase and phosphatidylserine the largest decrease in terms of the (18:0 + 18:1 + 18:2)/18:3 ratio (Table 2 and 3).

There are thus obvious differences between maize- and sunflower-treated seedlings. In maize, linolenic acid biosynthesis in the major glycolipids MGD and DGD is greatly inhibited, whereas in sunflower the glycolipids affected are the minor glycosylated sterol components, ESG + SG. It would appear that linolenic acid biosynthesis in MGD and DGD is very important for the normal plant, since inhibition of linolenic acid biosynthesis has a severe effect on plants.

It is known, however, that certain pyridazinone herbicides that are potent inhibitors of carotenoid synthesis and chlorophyll accummulation also interfere with membrane lipid formation. The major primary effect of these herbicides seems to be the almost total inhibition of colored carotenoids through interference with the desaturation steps (Bartels and McCullough 1972). Photooxidation of chlorophylls, as a consequence of the absence of carotenoids, has been suggested as the mode of action of these herbicides. St. John (1982) has shown further that pyridazinone herbicides act at multiple sites. The possibility thus arises that actions at some sites may be the secondary consequences of action at other sites. So, in the present study, the inhibiting effect of Perfluidone on the desaturase activity leading to linolenic formation in maize may be either the primary or the secondary effect of the action of this herbicide. Further studies will have to be carried out to determine the effect, if any, of inhibition of linolenic acid biosynthesis on chloroplast membrane function and how this interferes with the normal growth of seedlings.

In summary, Perfluidone is much more effective in maize than in sunflower seedlings. The most obvious differences are the various growth parameters, which are greatly affected in maize, as are the contents of the chlorophyll and carotenoid pigments and the desaturase steps leading to linolenic acid for-

**Table 3.** Effect of Perfluidone on fatty acid composition of phospholipids in maize and in sunflower. Results are given as mole % of total fatty acids.

| | | 16:0 | 16:1[b] | 18:0 | 18:1 | 18:2 | 18:3 | 20:0–22:0[c] | 18:2/18:3 | 18:0 + 1 + 2/18:3 |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | *PG* | | | | |
| Maize | (Con[a]) | 24.1 | 2.7 | 8.8 | 16.3 | 43.5 | 3.7 | 0.9 | 11.76 | 18.5 |
| | (Herb) | 27.4 | 7.8 | 16.8 | 25.3 | 19.2 | 3.5 | — | 5.48 | 17.5 |
| Sunfl | (Con) | 9.5 | 2.2 | 4.0 | 19.2 | 61.9 | 3.2 | — | 19.34 | 26.6 |
| | (Herb) | 8.5 | 2.1 | 4.2 | 18.1 | 62.9 | 4.2 | — | 14.97 | 20.3 |
| | | | | | | *PC* | | | | |
| Maize | (Con) | 19.0 | 0.5 | 9.8 | 12.9 | 44.2 | 11.5 | 2.1 | 3.84 | 5.82 |
| | (Herb) | 23.6 | 0.9 | 4.3 | 5.9 | 60.6 | 4.7 | — | 12.89 | 15.06 |
| Sunfl | (Con) | 22.6 | 0.8 | 11.3 | 15.5 | 44.1 | 3.6 | 2.1 | 12.25 | 19.7 |
| | (Herb) | 28.3 | 1.2 | 8.7 | 3.8 | 52.9 | 5.1 | — | 10.37 | 12.8 |
| | | | | | | *PE* | | | | |
| Maize | (Con) | 10.8 | 1.1 | 6.0 | 11.9 | 47.9 | 18.6 | 3.7 | 2.57 | 3.53 |
| | (Herb) | 14.4 | 2.5 | 4.3 | 8.8 | 52.9 | 13.8 | 3.3 | 3.83 | 4.78 |
| Sunfl | (Con) | 11.5 | 0.5 | 4.7 | 10.3 | 56.5 | 15.6 | 0.9 | 3.62 | 4.58 |
| | (Herb) | 8.8 | 1.0 | 4.5 | 12.0 | 51.3 | 22.3 | 1.0 | 2.30 | 3.04 |
| | | | | | | *PI* | | | | |
| Maize | (Con) | 18.0 | — | 10.7 | 19.3 | 29.5 | 22.5 | — | 1.31 | 2.64 |
| | (Herb) | 16.0 | — | 15.1 | 20.2 | 30.5 | 18.2 | — | 1.67 | 3.61 |
| Sunfl | (Con) | 17.9 | 5.0 | 11.8 | 13.3 | 46.7 | 3.1 | 2.2 | 15.06 | 23.2 |
| | (Herb) | 21.4 | 4.6 | 11.9 | 14.0 | 39.9 | 3.0 | 5.0 | 13.30 | 21.9 |
| | | | | | | *PS* | | | | |
| Maize | (Con) | 17.1 | 6.3 | 11.2 | 17.8 | 34.3 | 3.5 | 9.8 | 9.80 | 18.1 |
| | (Herb) | 24.5 | 11.1 | 8.9 | 19.5 | 28.9 | 4.1 | 3.0 | 7.04 | 14.0 |
| Sunfl | (Con) | 20.1 | 3.4 | 12.8 | 19.5 | 42.4 | 1.8 | — | 23.55 | 41.3 |
| | (Herb) | 19.3 | 5.3 | 17.3 | 19.0 | 30.6 | 3.9 | — | 7.85 | 17.2 |

[a] Con = control; Herb = herbicide; Sunfl = sunflower.
[b] Includes $\Delta^3$-trans isomer only in PG, in addition to the $\Delta^9$-isomer.
[c] Includes 20:0, 20:1, 20:3, 20:4, and 22:0.

**Table 4.** Effect of Perfluidone on fatty acid composition of neutral lipids in maize and in sunflower. Results are given as mole % of total fatty acids.

| | | 16:0 | 16:1 | 18:0 | 18:1 | 18:2 | 18:3 | 20:0–22:0[b] | 18:2/18:3 | 18:0 + 1 + 2/18:3 |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | *FA + FA esters* | | | | |
| Maize | (Con[a]) | 13.0 | 2.4 | 8.4 | 20.0 | 52.1 | 3.3 | 0.8 | 14.5 | 24.4 |
| | (Herb) | 14.7 | 1.1 | 7.4 | 21.9 | 51.2 | 3.6 | 0.1 | 14.2 | 22.4 |
| Sunfl | (Con) | 8.9 | 2.2 | 7.4 | 15.9 | 54.1 | 2.0 | 9.5 | 27.1 | 38.7 |
| | (Herb) | 8.5 | 3.8 | 6.6 | 16.0 | 56.3 | 2.5 | 6.3 | 22.5 | 31.6 |
| | | | | | | *Triglycerides* | | | | |
| Sunfl | (Con) | 11.0 | 5.1 | 8.1 | 21.6 | 47.2 | 2.8 | 4.2 | 16.9 | 27.5 |
| | (Herb) | 17.1 | 7.1 | 9.6 | 24.3 | 38.9 | 1.5 | 1.5 | 25.9 | 48.5 |
| | | | | | | *Unknown* | | | | |
| Sunfl | (Con) | 14.5 | 2.8 | 11.5 | 21.6 | 47.3 | 0.7 | 1.6 | 67.6 | 114.9 |
| | (Herb) | 15.0 | 4.7 | 10.6 | 17.6 | 42.9 | 6.1 | 4.1 | 7.0 | 11.6 |
| | | | | | | *Diglycerides* | | | | |
| Maize | (Con) | 31.2 | 4.0 | 19.5 | 14.0 | 24.8 | 2.8 | 3.7 | 8.9 | 20.8 |
| | (Herb) | 30.4 | 2.6 | 21.3 | 14.8 | 25.9 | 2.4 | 2.6 | 10.8 | 19.7 |
| Sunfl | (Con) | 11.5 | 1.7 | 9.1 | 20.7 | 45.8 | 2.3 | 8.9 | 19.9 | 32.9 |
| | (Herb) | 19.0 | 1.9 | 7.3 | 16.0 | 49.2 | 3.3 | 3.3 | 14.9 | 21.2 |
| | | | | | | *Monoglycerides* | | | | |
| Maize | (Con) | 19.9 | 11.5 | 24.0 | 13.8 | 24.4 | 6.4 | — | 3.8 | 9.7 |
| | (Herb) | 22.7 | 11.6 | 14.4 | 18.4 | 25.1 | 6.7 | 1.1 | 3.8 | 8.6 |
| Sunfl | (Con) | 20.0 | 4.3 | 13.7 | 15.5 | 39.0 | 6.6 | 0.9 | 5.9 | 10.3 |
| | (Herb) | 21.3 | 3.8 | 9.9 | 16.2 | 37.7 | 10.5 | 0.6 | 3.6 | 6.1 |

[a] Con = control; Herb = herbicide; Sunfl = sunflower.
[b] Includes 20:0, 20:1, 20:3, 20:4, and 22:0.

mation in the major glycolipids MGD and DGD of chloroplasts, which are inhibited to a much lesser extent in sunflower.

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