Stress-Protective Role of Long Chain Fatty Acids in Barley Springs under the Action of Electromagnetic Field of Extreme High Frequency

Ekaterina P. KONDRALENKO
Ph.D. (in Agriculture)
Professor
Kuzbass State Agricultural Academy
5, Markovtsev Str., Kemerovo, 650056, Russia

Olga M. SOBOLEVA
Ph.D. (in Biology)
Associate Professor
Kemerovo State Medical University
22a, Voroshilov Str., Kemerovo, 650056, Russia

Andrey S. SUKHIKH
Ph.D. (in Pharmaceutics)
Senior Researcher
Kemerovo State Medical University
22a, Voroshilov Str., Kemerovo, 650056, Russia

Iraida A. SERGEYVA
Ph.D. (in Physical and Mathematical Sciences)
Associate Professor
Kuzbass State Agricultural Academy
5, Markovtsev Str., Kemerovo, 650056, Russia

Julia V. ZAKHAROVA
Ph.D. (in Medical Sciences)
Associate Professor
Kemerovo State Medical University
22a, Voroshilov Str., Kemerovo, 650056, Russia
Abstract

The article shows the response of barley seeds to the influence of an electromagnetic field of ultrahigh frequency (EMF microwave). The action of microwave EMF leads to a change in the qualitative and quantitative composition of fatty acids contained in the organs of barley seedlings. The main saturated fatty acids that make up barley seed lipids are palmitic, and among unsaturated ones are oleic and linolenic acids. The content of other higher aliphatic acids is low. The maximum changes under the influence of microwave EMF occur in the sprouts and roots of seedlings with an increase in the number of carbon atoms in the fatty acid molecule. The most important for the growth and development of leaves is saturated hexacosan fatty acid with 26 carbon atoms, for roots – unsaturated aceterucic C24:1, for endosperm – saturated tricocylic acid with an odd number of carbon atoms (C23:0). Synthesis of long-chain fatty acids plays an important role in cell growth. Changes in the content of such compounds affect the development of embryos, leaves, and roots. Long-chain fatty acids are involved in regulating cell size, cell division, and cell differentiation.

Keywords: barley; seedlings; electromagnetic field of ultrahigh frequency; long chain fatty acids.

Introduction

Fatty acids (FAs) are open-chain aliphatic monobasic carboxylic acids found primarily in esterified form in fats, oils and waxes of plant and animal origin. FAs contain an unbranched chain of carbon atoms and can be either saturated or unsaturated. According to the length of the carbon chain, FAs are divided into short-chain (from C4 to C6), medium-chain (from C7 to C14) and long-chain (more than C15).

Short chain fatty acids are intermediates in the synthesis or degradation of longer chain fatty acids. They are not components of biological membranes. Since high concentrations of free fatty acids can have a toxic effect on the cell, these molecules are stored as triacylglycerolipids. Non-polar triacylglycerolipids do not perform a structural function; they accumulate in seeds as reserve energy compounds.

Higher fatty carboxylic acids are part of polar phospholipids, glycolipids and neutral triacylglycerolipids. Polar phospholipids play a structural role. Glycerophospholipids are the main components of the membranes of the cell and its organelles. Phosphatidylinositol plays an important role in the phospholipid-calcium metabolism of hormonal signal transmission to the cell. The composition of these compounds includes fatty acids containing C14 - C24 carbon atoms (Stillwell, 2018).
Fatty acids with a very long chain have a length of C_{20} carbon atoms with varying degrees of saturation (Zhukov, 2018). These FAs occupy an independent metabolic niche in many important biological processes. Very long-chain fatty acids formed in plants are components or precursors of numerous specialized metabolites synthesized in individual cell types.

Very long chain fatty acids are also membrane components and make up 5-10% of the acyl lipids of the plasma membranes of higher plants. Such organic acids are part of sphingolipids, which, like phospholipids, are important structural components of membranes. In addition, complex sphingolipids are potential reservoirs of signaling molecules (Gromnier et al., 2016) and show significant changes in the content of fatty acids with a long C-chain after stress.

Scientific studies in the field of clarifying the role of long chain fatty acids and their derivatives have convincingly proved that in the cell under stress they act as signaling molecules (De Bigault Du Granrut, Cacas, 2016; Lim et al., 2017). Long chain fatty acids formed in plants are components or precursors of numerous specialized metabolites synthesized in individual cell types (Li et al., 2016).

Despite the large number of works devoted to the influence of electromagnetic fields of ultrahigh frequency (EMF microwave) on living organisms, the mechanism of their action has not been finally clarified, which determines the relevance of research.

In connection with the foregoing, the aim of the research was set to establish the response of barley seedlings to the influence of microwave EMF.

**Methods**

The object of research was seedlings of spring barley sowing (*Hordeum sativum L.*) of variety Nikita. The experimental scheme included two options: *control* — without processing, and *experiment* — electromagnetic irradiation of ultrahigh frequencies with a power - 0.42 kW, frequency - 2.45 GHz, and exposure time - 11 sec. After treatment of dry barley seeds and its germination for 7 days, all the anatomical parts of the seedlings (sprouts, roots, endosperm, membranes) were extracted with a mixture of chloroform: n-hexane in the published sample preparation mode (Zakharova, Sukhikh, 2015). The preparation of fatty acid methyl esters was carried out as follows: a 1 ml sample was placed in a 1.5 ml vial, and the solvent mixture was blown off with nitrogen to dryness; 500 μl of sodium methylate in MeOH prepared according to GOST R 51486-99 was added to the residue and heated at 900 °C for 15 min, then 750 μl of a 3%-solution of H₂SO₄ in methanol and 100 μl of toluene were added. An internal standard (5 μg of methylundecanoate) was added to the resulting solution. Then, the sample was heated at 90 °C for 60 min. Next, 700 μl of n-hexane was extracted (in three portions). The combined extracts were
washed with double distilled water. The hexane fraction was concentrated by blowing off the solvent to a volume of about 50 μl. The resulting sample containing methyl ester fatty acids was used for analysis. The analysis was carried out on a mass spectrometer “Agilent 7000B” (USA). The sample volume was 2 μl, injection without dividing the flow. Column: ZB-WAX, 30m*0.25mm*0.25μm.

Chromatography conditions: Oven Program at 100 °C from 0 min, heated 7 °C/min to 260 °C for 10 min, flow rate 1.2 ml/min. Identification was carried out by mass spectra (library of mass spectra NIST 02.L) and retention indices. The calculation of the mass content of methyl esters of acids was carried out relative to the known amount of methylundecanoate (internal standard). Calibration was performed using standard samples (Sigma-Aldrich), consisting of chains of various lengths and saturations (8:0; 16:0; 18:1; 20:4; 22:6).

All measurements were performed in triplicate biological and triplicate analytical replicates; the tables show the averages. The results were processed statistically - the significance of differences compared with the control was found by the F-criterion at a significance level of 0.05 (in the tables, significant differences are indicated by *).

Results

In the course of the current study, the effect of microwave electromagnetic fields on the metabolism of fatty acids in the tissues and organs of barley seedlings was evaluated. It is known that under the influence of this abiotic factor, the metabolism of not only proteins, lipids, carbohydrates, but also the compounds of their components can change. The impact of microwave EMF on the production of fatty acids in seedling organs was assessed for the first time and provided new information on the mechanism of action of microwave EMF.

At the first stage of the study, there was analyzed the change in the qualitative composition of fatty acids in the leaves, roots, endosperm, and membranes of barley seedlings under the action of microwave electromagnetic fields (Table 1). The main fatty acids in all organs of barley seedlings are palmitic, oleic and linolenic acids. A specific feature of the fatty acid composition of barley seedlings is organ-specificity.

Table 1. Change in the production of saturated and unsaturated fatty carboxylic acids in seedlings under the action of microwave EMF, % out of their total amount

| Seedling Organs | sprouts | roots | endosperm | membranes |
|-----------------|---------|-------|-----------|-----------|


It was found that the difference in FAs content between untreated (control) and processed (experiment) before sowing seeds in conditions of microwave EMF is significant. The study of the fatty acid composition of the organs of barley seedlings showed that the concentration of all the studied saturated fatty acids in the sprouts, roots, endosperm and membranes decreased under the action of microwave EMF, reaching a minimum in the endosperm. According to the analysis of the data in Table 1 it follows that the percentage of saturated FAs in the endosperm decreases after processing the microwave EMF more than 10 times. A strong decrease was noted in the palmitic acid content. Its percentage drops from 77.9% to 0.41%. At the same time, the opposite effect is observed for unsaturated FAs. It was found that the treatment of microwave EMF leads to an increase in the percentage of unsaturated FAs, mainly oleic, linoleic and linolenic acids. It was noted that in the endosperm, oleic acid production is enhanced from 2.7% to 83% (almost 30 times).

Therefore, the effects of exposure to barley seeds on the microwave electromagnetic field in the endosperm are enhanced synthesis of unsaturated oleic acid from saturated palmitic. It should be noted that in all the organs of seedlings there is a tendency to a decrease in the number of saturated FAs and an increase in the production of unsaturated ones.

| Fatty Acid          | control | experiment | control | experiment | control | experiment | control | experiment |
|---------------------|---------|------------|---------|------------|---------|------------|---------|------------|
| Myristic C14:0      | 1.675   | 1.518      | 2.076   | 1.039      | 0.341   | 0.268      | 0.590   | 0.478      |
| Pentadecane C15:0   | 0.824   | 0.113*     | 1.242   | 1.055*     | 0.093   | 0.126*     | 0.213   | 0.151*     |
| Palmitic C16:0      | 45.127  | 21.252*    | 40.280  | 52.652*    | 42.079  | 0.410*     | 35.126  | 30.644*    |
| Margarine C17:0     | 0.374   | 0.477*     | 0.432   | 0.271*     | 0.098   | –          | –       | 0.098      |
| Stearic C18:0       | 5.216   | 5.568      | 13.627  | 4.845      | 5.253   | 5.679      | 1.887   | 1.754      |
| Arachin C20:0       | 3.190   | 3.935*     | 1.972   | 2.093      | 0.197   | 0.347      | 0.343   | 0.468*     |
| Behenic C22:0       | 5.314   | 7.181      | 4.474   | 5.311      | 0.021   | –          | –       | 0.051      |
| Tricosyl C23:0      | –       | 0.893*     | 0.923   | 0.964      | 0.438   | 0.347      | 0.390   | 0.843*     |
| Lignoceric C24:0    | 4.924   | 6.551      | 8.475   | 12.232     | 0.066   | 1.149*     | 0.118   | 0.162*     |
| Hexacosan C26:0     | 7.348   | 20.357     | 3.384   | 2.859      | 0.574   | 0.126*     | 0.390   | 0.668      |
| 9-methyltetradecane | 0.174   | 0.328      | 0.224   | 0.211      | 0.215   | 0.535      | 0.189   | 0.304      |
| Myristelaidic C14:1 | 0.254   | 0.586      | –       | 0.225      | 0.015   | 0.048      | 0.024   | 0.025      |
| Palmitolein C16:1   | 2.824   | 3.112      | 3.052   | 0.754      | –       | 0.032      | 0.036   | 0.035      |
| Heptadecamonoenoic C17:1 | 0.205 | 0.312*     | 0.209   | 0.423*     | 0.453   | 4.373*     | 0.272   | 0.320      |
| Oleic C18:1         | 6.394   | 6.982      | 5.298   | 7.101      | 4.031   | 83.271     | 9.295   | 11.414*    |
| Ecosene C20:0       | –       | 0.655*     | 0.361   | 0.543      | 0.162   | 0.048      | 0.284   | 0.360      |
| Erucylacetic C24:1  | 0.528   | 0.774      | –       | 0.724      | 0.106   | 1.258      | –       | 0.209      |
| Linoleic C18:2      | 7.756   | 8.532      | 10.935  | 5.191      | 44.936  | 1.479      | 49.651  | 50.184     |
| Isomer of linoleic acid C18:2 | – | 0.454 | – | 0.438 | – | 0.079 | – | 0.110 |
| Linolenic C18:3     | 7.873   | 9.420      | 3.036   | 1.069      | 0.922   | 0.425      | 1.192   | 1.722      |

* The differences are significant at p ≤ 0.05
It was revealed that for the organs of barley seedlings, there is a significant change in the production of both saturated and unsaturated FAs after treatment with microwave EMF. Thus, the treatment enhances the metabolic processes in the organs of the seedling.

There was calculated the proportion of individual fatty acids in the organs of seedlings in the control and experimental version (Table 2). Analysis of the data in Table 2 showed that the proportion of long chain fatty acids after treatment increases. Thus, for example, no tricyclic acid was found in the leaves in the control variant; its production increased in the experimental one: its share was 1.31%. The increase in the content of behenic acid was by 1.4 times, margarine and arachinic acid – by 1.3 times, 9-methyl tetradeanoic - by 2 times.

Table 2. The proportion of fatty acids in the organs of seedlings, %

| Fatty Acid          | Sprouts | Root | Endosperm | Membranes |
|---------------------|---------|------|-----------|-----------|
| Myristic C14:0      | 2.24    | 2.18 | 2.85      | 1.24      |
| Pentadecane C15:0   | 1.12    | 1.58 | 1.68      | 1.26      |
| Palmitic C16:0      | 60.86   | 30.70| 54.52     | 43.04     |
| Margarine C17:0     | 0.53    | 0.71 | 0.53      | 0.32      |
| Stearic C18:0       | 7.00    | 8.06 | 16.65     | 5.80      |
| Arachin C20:0       | 4.30    | 5.66 | 2.41      | 2.50      |
| Behenic C22:0       | 7.18    | 10.40| 5.67      | 6.36      |
| Tricocyl C 23:0     | 0.00    | 1.31 | 1.12      | 1.15      |
| Lignoceric C 24:0   | 6.65    | 9.47 | 10.36     | 14.66     |
| Hexacosan C26:0     | 9.89    | 29.45| 4.12      | 3.42      |
| 9-methyltetradecane | 0.24    | 0.49 | 0.29      | 0.25      |

Analysis of the table 2 shows that among saturated FAs, palmitic acid with an even number (C 16) of carbon atoms has the greatest influence on the growth and development of seedlings. In sprouts, its content in the experimental version is reduced by 2 times, in the endosperm - by 19 times (Figure 1).
Figure 1. Content of saturated fatty acids in barley seedlings depending on C-atom number

With an increase in the number of C-atoms (Figure 2), the difference between the control and the experimental variant increases. So, for example, there is a 3-fold increase in the synthesis of hexacosanoic fatty acid.

Figure 2. Content of saturated long chain fatty acids in the organs of barley seedlings

Figure 3 shows the dependences of the unsaturated FA content on carbon atoms’ number in their molecules in different organs of the seedling. For all the studies performed, it was found that both in the control samples and after exposure to microwave EMF in all the organs of the seedlings, heptadecamonoenoic acid content with an odd number of carbon atoms has a minimum content (C17:1). It follows that its influence on the growth and development of barley seedlings is insignificant.
Figure 3. The dependence of unsaturated FA content (μg/ml) on the number of carbon atoms in their molecules

For all the studied organs of barley seedlings, the change in the ratio of the concentration of saturated fatty acids to unsaturated was calculated (Table 3).

**Table 3. Changes in the ratio of concentrations of saturated FA (P) to unsaturated FA (S) in the organs of barley seedlings under the influence of microwave EMF**

| Index P/S | sprouts | roots | endosperm | membranes |
|-----------|---------|-------|-----------|-----------|
|           | control | experiment | control | experiment | control | experiment |
|           | 2.06    | 1.6    | 9.82      | 3.19      | 6.79    | 0.05       | 0.56      | 0.46      |

An analysis of the obtained data shows that the proportion of saturated FAs in the composition of fatty acids decreases under the influence of microwave electromagnetic fields in all organs of the seedling. Therefore, it can be argued that saturated FAs are primarily disposed of.

Based on the analysis of the data obtained, the correlation coefficients between the content of saturated FAs and the number of carbon atoms in their molecules and in the organs of barley seedlings were calculated. As can be seen from the data presented, for all saturated FAs, the value of the correlation coefficient on the number of carbon atoms in their molecules is almost equal to unity, which indicates a direct effect of the carbon chain length in FA molecules on the qualitative composition of fatty acids in seedling organs.
Table 4 presents data on the relative change in the content of saturated and unsaturated fatty acids in the organs of seedlings under the influence of microwave electromagnetic fields. It was established that the maximum accumulation of oleic with one and linoleic with two double bonds in the FA molecule occurs in the endosperm and membrane when exposed to microwave EMF on barley seeds.

Table 4. The effect of microwave EMF on the content change of saturated and unsaturated fatty acids in the organs of seedlings

| Fatty acid          | sprouts | roots | endosperm | membranes |
|---------------------|---------|-------|-----------|-----------|
| Myristic C14:0      | 1.0526  | 0.7113| 0.3542    | 0.9000    |
| Pentadecane C15:0   | 1.5263  | 1.2281| 0.6154    | 0.7778    |
| Palmitic C16:0      | 0.5455  | 1.8894| 0.0044    | 0.9752    |
| Margarine C17:0     | 1.4444  | 1.0000| 0.0000    | 0.09/0    |
| Stearic C18:0       | 1.2437  | 0.5689| 0.5404    | 1.0375    |
| Arachin C20:0       | 1.4247  | 1.6951| 0.9167    | 1.5172    |
| Behenic C22:0       | 1.5656  | 1.8978| 0.4000    | 1.6061    |
| Tricocyl C23:0      | 0.24/0* | 1.6842| 9.1250    | 1.0000    |
| Lignoceric C24:0    | 1.5398  | 2.3125| 0.1111    | 1.2727    |
| Hexacosan C26:0     | 3.2202  | 1.3571| 1.2593    | 1.1875    |
| Myristelaidic C14:1 | 2.6667  | 0.15/0*| 0.02/0*  | 1.0000    |
| Palmitolein C16:1   | 1.2769  | 1.0000| 12.0870   | 1.3043    |
| Heptadecamonoenoic C17:1 | 1.6000 | 9.3333| 0.0000    | 0.04/0    |
| Oleic C18:1         | 1.2671  | 5.3636| 25.9461   | 1.3731    |
| Eicosene C20:0      | 0.17/0  | 6.0000| 0.3333    | 1.4167    |
| Erucylacetic C24:1  | 1.7500  | 0.48/0 | 16.0000   | 0.13/0    |
| Linoleic C18:2      | 1.4103  | 4.4150| 23.4689   | 1.3914    |
| Isomer of linoleic acid C18:2 | 0.12/0* | 0.29/0* | 0.0000 | 0.0000 |
| Linolenic C18:3     | 1.2825  | 8.4146| 0.1815    | 1.1297    |

* - the numerator shows the value after irradiation, the denominator – the value after irradiation

From the analysis of Table 4 it is seen that the microwave EMF has a significant effect on fat metabolism in the organs of barley seedlings. It was revealed that there is an increase in the content of both saturated and unsaturated fatty acids in sprouts from 1.5 to 3 times, in roots by 9 times. In the control variant, tricyclic fatty acid was not found in the sprouts, after exposure to EMF seeds, the production of this acid is observed, and in the endosperm it was by 9 times lower. Basically, in the endosperm, a decrease in fatty acids occurs.

In the membranes, the content of fatty acids with the number of C-atoms decreases to 17. Both saturated and unsaturated long chain fatty acids increase by 20-60%. As can be seen from the
data presented, the highest content after exposure to radiation is oleic acid in the endosperm and linoleic with two double bonds in the membranes.

When calculating the concentration ratio of ω-6 to ω-3 acids (linoleic to linolenic) after exposure to microwave EMF, the sprouts and roots of seedlings practically does not change, while in the endosperm and membranes there is a significant decrease. So, for the endosperm, the concentration ratio decreases by 15 times, and in the membranes - by 1.5 times. It was shown that after irradiation, linoleic acid is used to the maximum in these organs for the growth and development of seedlings.

The synthesis of long chain FAs plays an important role in cell growth (Zheng et al., 2005). Changes in the content of long chain high fatty acids affect the development of embryos, leaves, and roots. According to the statement (Bach et al., 2011), long C-chain fatty acids are involved in the regulation of cell size, cell division and their differentiation.

There was calculated the percentage of long chain FAs (C_{20-26}) of their total number (Table 4). A noticeable shift in the fatty acid composition is probably an urgent problem regarding the effect of microwave electromagnetic fields on signaling pathways.

An analysis of the data in Table 5 shows that the effect of microwave EMF on barley seeds leads to an increase in the production of barley sprouts of arachin, behenic, tricocyl, lignoceric, especially hexacosan long chain FAs. The synthesis of behenic, eicosenic, erucylacetic, especially lignoceric FAs in the roots of seedlings is intensifying. Organ specificity was revealed in the production of long chain FAs after treatment of barley seeds with microwave EMF.

Table 5. Change in the production of long chain fatty acids of barley seeds under the action of microwave EMF, % of their total amount

| Fatty acid       | sprouts | roots | endosperm | membranes |
|------------------|---------|-------|-----------|-----------|
|                  | control | experiment | control | experiment | control | experiment | control | experiment |
| Arachin C_{20:0} | 3.2     | 3.9    | 2.3       | 2.1       | 0.3     | 0.3        | 0.3     | 0.5        |
| Behenic C_{22:0} | 5.3     | 7.2    | 5.2       | 5.8       | 0.7     | 0.8        | 0.4     | 0.6        |
| Tricocyl C_{23:0}| 0       | 0.9    | 1.1       | 1.0       | 0.1     | 1.1        | 0.1     | 0.1        |
| Lignoceric C_{24:0} | 4.9 | 6.5    | 9.8       | 12.2      | 0.9     | 0.1        | 0.4     | 0.4        |
| Hexacosan C_{26:0} | 7.3 | 20.3   | 3.9       | 2.9       | 0.4     | 0.5        | 0.2     | 0.2        |
| Eicosenic C_{20:0} | 0      | 0.6    | 0.2       | 0.5       | 0.1     | 0.0        | 0.3     | 0.4        |
| Erucylacetic C_{24:1} | 0.5 | 0.8    | 0         | 0.7       | 0.1     | 1.3        | 0       | 0.1        |
| Total FAs, %     | 21.7    | 40.2   | 43.2      | 22.5      | 2.6     | 4.1        | 1.7     | 1.9        |
Discussion

From the scientific literature it is known that free long chain fatty acids contribute to the regulation of organ and tissue homeostasis. They act as signaling molecules. The extracellular free concentration of these fatty acids can be perceived by protein-bound free fatty acid receptors (Ichimura et al., 2014). In addition, it was reported about the participation of a number of long chain acyl-CoA-binding proteins in plant resistance to stress (Xiao, Chye, 2011). Scientific studies suggest that they function as general regulators of lipid metabolism. Sphingolipids contain most of the long chain fatty acids produced in leaves (Pata et al., 2010; Cacas et al., 2016). This helps to explain the mechanism of the participation of long chain fatty acids in the stress signaling reaction in plant cells.

Based on the scientific literature, the reason for the relatively high amounts of long C-chain fatty acids observed in sprouts and roots of barley under the influence of microwave electromagnetic fields can be suggested. It is likely that under stress this is a response of the seedlings to the effect of the indicated abiotic factor.

There was calculated the ratio of the content of long chain FAs in the experiment to the control in the organs of barley seedlings (Table 6).

**Table 6. The content ratio of long chain FAs of experiment/control in seedling organs after irradiation**

| Number of C-atoms | sprouts | roots | endosperm | membranes |
|------------------|---------|-------|-----------|-----------|
| C<sub>20</sub>   | 1.42    | 1.70  | 0.92      | 1.52      |
| C<sub>22</sub>   | 1.57    | 1.90  | 0.40      | 1.61      |
| C<sub>23</sub>   | 1.00    | 1.68  | 9.13      | 1.00      |
| C<sub>24</sub>   | 1.54    | 2.31  | 0.11      | 1.27      |
| C<sub>26</sub>   | 3.22    | 1.36  | 1.26      | 1.19      |

As follows from the experimental data, after treatment of barley seeds before sowing under conditions of microwave EMF, the most significant increase in the content of long chain FAs was detected in endosperm, roots and sprouts. It was established that saturated hexacosan FA with 26 carbon atoms is the most significant for leaf growth and development; unsaturated erucylacetic C24:1 FA - for roots; saturated tricocyl (C 23:0) with an odd number of carbon atoms - for endosperm. As for membranes, this effect is less significant.
Conclusion

Thus, the studies conducted allowed establishing the response of barley seeds to the influence of microwave electromagnetic fields - the stress-protective role of fatty acids with a long carbon chain. The action of microwave EMF leads to a change in the qualitative and quantitative fatty acid composition of the organs of barley seedlings when exposed to microwave EMF. Based on the results obtained, it can be concluded that the main saturated fatty acids that are part of barley seed lipids are palmitic, and among unsaturated ones are oleic and linolenic acids. The content of other FAs is low. The maximum changes under the influence of microwave EMF occur in the sprouts and roots of seedlings with an increase in the number of carbon atoms in the FA molecule.

References

Bach, L., Gissot, L., Marion, J., Tellier, F., Moreau, P., Satiat-Jeunemaître, B., Palauqui, J.C., Napier, J.A., Faure, J.D. (2011). Very-long-chain fatty acids are required for cell plate formation during cytokinesis in Arabidopsis thaliana. *Journal of cell science*, 124(19), 3223-3234. [http://doi.org/10.1242/jcs.074575](http://doi.org/10.1242/jcs.074575)

Cacas, J.L., Buré, C., Grosjean, K., Gerbeau-Pissot, P., Lherminier, J., Rombouts, Y., Maes, E., Bossard, C., Gronnier, J., Furt, F., Fouillen, L., Germain, V., Bayer, E., Cluzet, S., Robert, F., Schmitter, J.M., Deleu, M., Lins, L., Simon-Plas, F., Mongrand, S. (2016). Revisiting plant plasma membrane lipids in tobacco: a focus on sphingolipids. *Plant physiology*, 170(1), 367-384. [https://doi.org/10.1104/pp.15.00564](https://doi.org/10.1104/pp.15.00564)

De Bigault Du Granrut, A., Cacas, J.L. (2016). How very-long-chain fatty acids could signal stressful conditions in plants? *Frontiers in plant science*, 7, 1490. [https://doi.org/10.3389/fpls.2016.01490](https://doi.org/10.3389/fpls.2016.01490)

Gronnier, J., Germain, V., Gouguet, P., Cacas, J.L., & Mongrand, S. (2016). GIPC: Glycosyl Inositol Phospho Ceramides, the major sphingolipids on earth. *Plant signaling & behavior*, 11(4), 1152438. [https://dx.doi.org/10.1080%2F15592324.2016.1152438](https://dx.doi.org/10.1080%2F15592324.2016.1152438)

Ichimura, A., Hasegawa, S., Kasubuchi, M., Kimura, I. (2014). Free fatty acid receptors as therapeutic targets for the treatment of diabetes. *Frontiers in pharmacology*, 5, 236.

Li, N., Xu, C., Li-Beisson, Y., Philippar, K. (2016). Fatty acid and lipid transport in plant cells. *Trends in Plant Science*, 21(2), 145-158. [https://doi.org/10.1016/j.tplants.2015.10.011](https://doi.org/10.1016/j.tplants.2015.10.011)
Lim, G.H., Singhal, R., Kachroo, A., Kachroo P. (2017). Fatty acid–and lipid-mediated signaling in plant defense. *Annual review of Phytopathology, 55*, 505-536. https://doi.org/10.1146/annurev-phyto-080516-035406

Pata, M.O., Hannun, Y.A., Ng, C.K.Y. (2010). Plant sphingolipids: decoding the enigma of the Sphinx. *New Phytologist, 185*(3), 611-630. https://doi.org/10.1111/j.1469-8137.2009.03123.x

Stillwell, W. (2018). *An introduction to biological membranes: from bilayers to rafts*. Elsevier.

Xiao, S., Chye, M.L. (2011). New roles for acyl-CoA-binding proteins (ACBPs) in plant development, stress responses and lipid metabolism. *Progress in lipid research, 50*(2), 141-151. https://doi.org/10.1016/j.plipres.2010.11.002

Zakharova, Y.V., Sukhikh, A.S. (2015). Chromatographic analysis of fatty acids of bifidobacteria cell walls with different hydrophobicity. *Sorption and Chromatographic Processes, 15*(6), 776-783. (in Russian)

Zheng, H., Rowland, O., Kunst, L. (2005). Disruptions of the Arabidopsis enoyl-CoA reductase gene reveal an essential role for very-long-chain fatty acid synthesis in cell expansion during plant morphogenesis. *The Plant Cell, 17*(5), 1467-1481. https://doi.org/10.1105/tpc.104.030155

Zhukov, A.V. (2018). Very long chain fatty acids in plant membrane lipids. *Plant physiology, 65*(6), 784-800. http://doi.org/10.1134/S1021443718050187