

Article ID: 169047
DOI: 10.5586/aa/169047

Publication History
Received: 2022-09-25
Accepted: 2023-02-10
Published: 2023-07-06

Handling Editor
Małgorzata Wójcik; Maria
Curie-Skłodowska University,
Lublin, Poland;
<https://orcid.org/0000-0001-6674-0341>


Funding
This research has been financed
from private fund.

Competing Interests
No competing interests have
been declared.

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ORIGINAL RESEARCH PAPER

Palmitic acid glyceride content in maize lines - carriers of the *wx* and *sh₁* mutations depending on the air temperature during the ripening period

Dmytro S. Tymchuk *

Kharkiv International Medical University, Molochna Str. 38, Kharkiv, 61001, Ukraine

* To whom correspondence should be addressed. Email: dstymchuk@yahoo.com

Abstract

In three-year experiments, we studied the effect of air temperature during grain ripening on the content of palmitic acid glycerides in the oils of corn (*Zea mays* L.) inbred lines of common type as well as inbred lines - carriers of *sh₁* and *wx* mutations of the endosperm structure. The material for the research was presented by 10 unrelated lines of each type, which were grown in the Steppe zone of Ukraine. The analysis of the fatty acid composition of the oil was carried out with the Peisker gas-chromatographic method. The evaluation of the genotype: environment interactions was carried out using the Eberhard–Russell method. It has been established that the lines - carriers of *sh₁* and *wx* mutations differ from the lines of common type in a higher level of palmitate content, and one of the probable causes for this may be the spatial linkage of the mutant *sh₁* and *wx* genes with the palmitate-coding locus of chromosome 9. Palmitate content in unrelated lines of each type varied depending on the genotype of the line and the norm of its response to temperature fluctuations during grain maturation. Some lines showed a significant range of palmitate content variability under different temperature regimes of the ripening period, while other lines had a fairly stable level of the trait under the same conditions. Lines with a stably elevated content of palmitate under contrasting temperature growing conditions were identified.

Keywords

Zea mays L.; *sh₁* and *wx* mutants; palmitate content in oil; effect of ripening temperature

1. Introduction

The main direction of genetic improvement of the quality of vegetable oils is to increase their content of oleic acid glycerides, which have significantly higher resistance to peroxidation than polyunsaturated acids (Merrill et al., 2008).

The improvement of vegetable oils, and corn oil in particular, in terms of oleate content has fully justified itself, being not only technically feasible but also yielding oils with high technological characteristics and a beneficial effect on human health (Büyüksolak, et al., 2020; Das et al., 2019; Karacor & Cam, 2015).

However, the improvement of corn in terms of oleate content does not cover all the prospects for optimizing the fatty acid composition of oil, which is created by intraspecific variability in the content of each of the main fatty acids that make up glycerides (Sanjeev et al., 2014). One of the promising ways to improve the quality of oils may be to change their content of palmitic acid (Pollak & Scott, 2005).

Palmitic acid is the quantitatively predominant saturated fatty acid, which is part of corn oil glycerides, and its share in the fatty acid composition of the oil can be considered as one of the significant factors determining oil properties (Karmakar et al., 2017).

However, the role of palmitate in the determination of various properties of oils is quite specific. On the one hand, the consumption of oils with a high content of palmitate provokes the occurrence of a number of diseases dangerous to human health (Manchini et al., 2015). On the other hand, oils high in palmitate significantly outperform oils high in unsaturated fatty acids in terms of resistance to lipid oxidation during heat treatment (Wiege et al., 2020). In addition, palmitic acid has a higher melting point than the monounsaturated and unsaturated acids found in the most common vegetable oils (Kenar et al., 2017).

Of practical importance are both a decrease and an increase in the content of palmitate in oil. Oils low in palmitate have been shown to inhibit or even prevent the development of a number of serious physiological disorders in the human body (Damude & Kinney, 2008). On the contrary, oils with high palmitate content provide a good alternative to hydrogenated fats, reducing the risk of highly undesirable trans-fatty acid isomers when they are obtained (White et al., 2007). Oils of this type can also be considered as promising sources of environmentally friendly lubricants (Salih & Salimon, 2021).

To date, mutations with a beneficial effect on palmitate content have been induced in major oilseeds. Genetic sources of increased palmitate content are known, in particular, in soybean and sunflower (Anai et al., 2012; Perez-Vich et al., 2016), and sources of reduced content are found in soybean and rapeseed (Coughlan et al., 2022; Lee et al., 2008).

Wide genotypic variability in palmitate content was also found in corn (Saini et al., 2020), which allows us to consider this crop as a potential industrial source of oils with high and low content of palmitic acid glycerides.

To date, eight palmitate-coding loci in chromosomes 1, 2, 4, 5, 6, 8, 9, and 10 have been found in maize, and the most expressive of them, providing 42% of the variability in palmitate content, is located on chromosome 9 (Yang et al., 2010). However, this locus does not have phenotypic markers of the allelic state, and the complicated methods of molecular genetic analysis were used to identify it, the use of which in the practical improvement of oil quality seems to be very difficult.

At the same time, maize chromosome 9 is known to contain mutant endosperm structure genes *sh₁* and *wx*, whose recessive alleles cause the formation of specific visually diagnosable grain phenotypes (Shannon et al., 2009) and can be spatially linked to the palmitate-coding locus of chromosome 9. However, the assumption that carriers of mutant *sh₁* and *wx* genes are also sources of increased palmitate content needs experimental confirmation.

On the other hand, it is known that the fatty acid composition of oils depends on the climatic conditions of growth and, in particular, on the temperature during the grain ripening period (Aguirrezabal et al., 2015). It has been shown that the content of palmitate increases with increasing temperature (Bellaloui et al., 2013), and this process has a non-linear character (Alsajri et al., 2020). However, it has not yet been established whether the nature of the relationship between the content of palmitate and temperature during the ripening period is common for all forms of this crop or whether changes in the content of palmitate at similar temperature fluctuations are specific to its various lines and varieties. Inbred lines with a phenotypically marked state of palmitate-coding loci should be recognized as the most suitable and practically significant objects for solving this problem.

Therefore, the objectives of this study were to experimentally test the effect of *sh₁* and *wx* endosperm mutations on the content of palmitate in corn oil and to establish the norms of reactions of various lines carrying these mutations to changes in the temperature of the ripening period in terms of the content of palmitate.

2. Material and methods

2.1. Plant material

The material for the study was presented by 10 unrelated corn inbred lines carrying the *sh₁* mutation (CS-03, CS-08, CS-09, CS-10, CS-13, CS-14, CS-15, CS-18, CS-21,

and CS-22) and 10 unrelated inbred lines carrying the *wx* mutation (BK-11, BK-13, BK-14, BK-19, BK-36, BK-37, BK-52, BK-64, BK-65, and BK-69). The controls were 10 common-type corn inbred lines that were not carriers of any of the above endosperm mutations (A-619, B-37, BC-70457, F-115, Oh-43, P-502, P-523, W-153, T-22, and W-64A).

The lines used in the experiments were obtained from the National Center for Plant Genetic Resources of Ukraine.

2.2. Location of the study

The field experiments were carried out at the breeding and seed station “NASCO”, which is located in the Novo-Kakhovsky district of the Kherson region and is part of the Steppe zone of Ukraine. Geographical coordinates of the site of the field experiments: 46.7545°N, 33.3486° E (Dateandtime.info, 2022).

2.3. Weather conditions

Corn lines were grown for three years (2013, 2016, and 2017), which differed in the temperature regime of the growing season and, in particular, in air temperatures during the period of grain ripening. The average temperature of this period was 19.9 °C in 2013, 21.7 °C in 2016, and 23.1 °C in 2017 (Pogodaiklimat, 2022).

2.4. Soils

The soils on the experimental plot were southern residual solonchic light loamy and medium loamy chernozems with humus content of 1.5%, soil acidity pH = 6.7, weighted average phosphorus content of 8.54 mg/100 g, and potassium content of 21.5 mg/100 g. The ecological and agrochemical score of the experimental site was 37.

2.5. Field research methods

When conducting field experiments, we were guided by the methodology of the National Center for Plant Genetic Resources of Ukraine (Gurieva et al., 2003). Corn lines were grown on single-row plots with the areas of 4.9 m², row spacings of 70 cm, and distances between plants in rows of 35 cm. The cultivation of corn lines was carried out in two-fold repetition and using the method of randomized repetitions.

For biochemical analysis, seeds of lines obtained exclusively by controlled pollination were used. For this purpose, within each plot, 3–4 female inflorescences were cross-pollinated with a mixture of pollen from 5–6 tassels of other plants in the same plot. The control of the allelic state of genes *sh₁* and *wx* was carried out according to the phenotype of the seed endosperm (Shannon et al., 2009).

2.6. Laboratory research methods

The analysis of the fatty acid composition of the oil was carried out according to the previously described method (Tymchuk et al., 2021). The extraction of oil from freshly ground seeds was carried out by petroleum ether at a temperature of 30 °C for 3 hours, after which the solvent was evaporated in a stream of nitrogen.

The resulting oil preparations were subjected to transesterification with a mixture of methanol:chloroform:sulfuric acid (100:100:1), and the resulting mixtures of fatty acid methyl esters were separated on a packed column of a Chrom-5 gas-liquid chromatograph (KOVO, Czech Republic). Silanized diatomite Inerton-AW-DMCS with a granule size of 0.16–0.20 mm served as a solid phase carrier for separation, and diethylene glycol succinate in an amount of 10% by weight of the solid carrier served as a liquid phase. High-purity nitrogen was used as the carrier gas.

Gas chromatographic analysis was carried out in the isothermal mode at a temperature of 190 °C using a flame ionization detector.

The components of the mixture to be separated were identified by the retention time of their peaks, established for reliable standards of fatty acid methyl esters (Sigma-Aldrich, USA).

2.7. Statistical analysis

The results obtained were subjected to statistical processing according to the previously described method (Dospikhov, 2011). Estimates of factors causing variability in the content of palmitate were carried out by calculating the values of the Fisher criterion for a 5% significance level ($F_{0.05}$). A comparison of the means for the experimental variants was carried out using the least significant difference for the 5% significance level ($LSD_{0.05}$).

To evaluate the genotype: environment interactions for palmitate content, we used a statistical program based on the Eberhard–Russell algorithm (Tymchuk et al., 2021). With its use, for each line, we calculated the genotypic effects (E_i) reflecting the average value of the trait over the years of testing, the linear regression coefficients (R_i) reflecting the response of the genotype to temperature fluctuations during maturation, and variances of trait stabilities (S_i^2) reflecting the reliability of estimates of line plasticity. To establish the significance of trait stabilities, the actual values of the Cochran G-test ($G_{\text{fact.}}$) were calculated and compared with the table ($G_{0.95}$).

Common corn lines and lines - carriers of each mutation were ranked according to E_i and R_i values into 3 groups, in which the lowest rank was assigned to lines with higher average levels of the trait and its lower dependence on temperature fluctuations during the ripening period.

3. Results

The results of the studies showed that, within the analyzed experimental complex, there is a fairly wide variability in the content of palmitate in the oil. Its sources were the genotypic differences between the lines and differences associated with the climatic conditions of the growing year. The line:year interactions also turned out to be significant in the lines carrying sh_1 and wx mutations (Table 1).

Table 1 Results of variance analysis for the palmitate content in the oils of corn inbred lines of the common type and lines – carriers of sh_1 and wx mutations according to estimates of 10 lines of each type in 2013, 2016, and 2017, calculated values of the criterion $F_{0.05}$.

Line types	Sources of variance		
	Inbred lines	Years	Interaction of factors
Common type	8.95	9.82	1.08
Carriers of mutation sh_1	21.16	4.85	5.13
Carriers of mutation wx	13.41	10.11	3.32
$F_{0.05 \text{ tab.}}$	2.21	3.32	1.96

The obtained results indicate that the corn lines - carriers of sh_1 and wx mutations differ from the lines of the common type by the higher content of palmitate in the oil. The lines carrying the sh_1 mutation analyzed in the experiments exceeded the lines of the common type by an average of 27.5%, and the lines carrying the wx mutation by 30.3%.

At the same time, the different lines of each of the three studied types of corn differed significantly from each other in terms of palmitate content, showing a rather wide intragroup quantitative variability of the trait (Table 2).

The results of the comparative assessment of the variability of the trait in the different groups of the analyzed lines showed that, in the carriers of the sh_1 and wx mutations, both the average level of palmitate content and the range of its intragroup variability are very close. However, although the carriers of the sh_1 and wx mutations had significantly higher average levels of the trait, compared to common corn, some lines carrying these mutations did not differ much from the lines of common corn in terms of palmitate content.

In all the groups of lines analyzed in the experiments, the highest average content of palmitate was found in the conditions of 2017 with the highest air temperature during

Table 2 Variability of palmitate content in the oils of corn inbred lines of common type and lines - carriers of sh_1 and wx mutations, results of analysis of lines grown in 2013, 2016 and 2017.

Line types	Palmitate content in the oil, %		
	Minimal	Maximal	Average
Common type	9.5	12.5	10.8
Carriers of mutation sh_1	11.7	16.0	13.8
Carriers of mutation wx	12.6	15.9	14.2
LSD _{0.05}	1.1	1.1	0.8

Table 3 Influence of the year of cultivation on the palmitate content in the oils of corn inbred lines of common type and lines - carriers of sh_1 and wx mutations, average results of evaluation of 10 lines of each type in 2013, 2016 and 2017.

Line types	Average palmitate content by years, %			LSD _{0.05}
	2013	2016	2017	
Common type	10.4	11.0	11.1	0.3
Carriers of mutation sh_1	13.5	14.0	14.0	0.4
Carriers of mutation wx	13.7	14.3	14.5	0.4

the period of grain ripening, and the lowest content of palmitate was found in the conditions of 2013 with the lowest temperature of this period (Table 3).

The analysis of all the three groups of lines analyzed in the experiments showed that the lines of each of them differ significantly from each other both in the average level of palmitate content and in the nature of its changes with temperature fluctuations during grain ripening.

In the lines of common type, the content of palmitate varied within 10.2–12.2%, according to the average results of the three-year tests. Lines BC-70457, Oh-43, and T-22 showed the lowest levels of the trait, and lines F-115 and P-523 showed the highest levels. The levels of palmitate content in the lines B-37, T-22, and W-64A showed a high dependence on fluctuations in air temperature during the ripening period, while lines F-115 and P-523 showed the most stable levels of the trait over the years (Table 4).

Similar patterns of palmitate content variability were also observed in the lines carrying the sh_1 and wx mutations, although their genetically determined level of palmitate content was higher than in the lines of the common type.

The content of palmitate in the lines carrying the sh_1 mutation varied in the range of 12.5–15.4%, according to the average three-year estimates. The lowest levels of the trait were recorded in the lines CS-08 and CS-14, while the highest levels were recorded in the lines CS-18 and CS-22. In the group of carriers of sh_1 mutation, the strongest dependence of the palmitate content on temperature during the ripening period was shown by the lines CS-03, CS-08, CS-10, CS-18, and CS-22, while the level of the trait in the lines CS-13, CS-15, and CS-21 was quite stable even under conditions of temperature fluctuations (Table 5).

In the lines carrying the wx mutation, the average content of palmitate ranged from 13.1 to 15.3%, according to the results of three-year tests. The lowest average levels of the trait were shown by the lines BK-11, BK-37, and BK-69, and the highest levels were shown by the lines BK-13 and BK-19. The content of palmitate in oil in the lines BK-14, BK-36, BK-52, and BK-65 changed quite significantly with fluctuations in air temperatures during the ripening period, while the lines BK-13, BK-19, and BK-37 showed significantly higher trait stability under these conditions (Table 6).

The calculated values of the Cochran test ($G_{\text{fact.}}$) for assessing the variability of the palmitate content in the analyzed groups of common corn lines as well as the carriers of the sh_1 and wx mutations were 0.3117, 0.1977, and 0.2800, respectively, and were

Table 4 Variability of palmitate content in the oils of corn inbred lines of common type grown in 2013, 2016, and 2017.

Lines	Palmitate content in the oil, %				Genotypic effects		Regression to variations in growing temperatures		Variance of trait stability, S_i^2
	2013	2016	2017	Average	E_i	Rank	R_i	Rank	
A-619	10.3	10.6	11.1	10.7	-0.21	2	0.95	2	0.09
B-37	10.4	11.7	11.3	11.1	0.26	2	1.66	3	0.15
BC-70457	9.9	10.6	10.5	10.3	-0.54	3	1.01	2	0.02
F-115	12.2	11.9	12.5	12.2	1.32	1	0.10	1	0.18
Oh-43	9.9	10.4	10.7	10.3	-0.54	3	1.08	2	0.02
P-502	10.8	11.5	11.4	11.2	0.36	2	1.01	2	0.02
P-523	11.5	11.9	10.9	11.4	0.56	1	-0.33	1	0.48
W-153	10.3	11.2	10.7	10.7	-0.14	2	0.94	2	0.17
T-22	9.5	10.1	10.9	10.2	-0.71	3	1.71	3	0.21
W-64A	9.8	10.5	11.3	10.5	-0.34	2	1.87	3	0.20
LSD _{0.05}		1.0		0.6	0.45	-	0.50	-	-

Table 5 Variability of palmitate content in the oils of corn inbred lines - carriers of mutation sh_1 grown in 2013, 2016, and 2017.

Lines	Palmitate content in the oil, %				Genotypic effects		Regression to variations in growing temperatures		Variance of trait stability, S_i^2
	2013	2016	2017	Average	E_i	Rank	R_i	Rank	
CS-03	12.3	14.0	13.7	13.3	-0.51	2	3.53	3	0.10
CS-08	11.7	12.3	13.4	12.5	-1.38	3	2.83	3	0.49
CS-09	13.8	13.4	14.7	14.0	0.12	2	0.79	2	0.81
CS-10	13.7	15.6	14.4	14.6	0.72	2	2.81	3	0.87
CS-13	14.5	13.3	12.3	13.4	-0.48	2	-4.09	1	0.35
CS-14	12.6	12.1	13.3	12.7	-1.18	3	0.42	2	0.70
CS-15	13.6	13.3	12.4	13.1	-0.75	2	-1.88	1	0.34
CS-18	13.7	16.0	15.6	15.1	1.25	1	4.79	3	0.18
CS-21	15.1	13.8	14.7	14.5	0.69	2	-1.82	1	0.48
CS-22	14.6	15.9	15.6	15.4	1.52	1	2.61	3	0.08
LSD _{0.05}		1.1		0.6	0.76	-	1.24	-	-

Table 6 Variability of palmitate content in the oils of corn inbred lines - carriers of mutation wx grown in 2013, 2016, and 2017.

Lines	Palmitate content in the oil, %				Genotypic effects		Regression to variations in growing temperatures		Variance of trait stability, S_i^2
	2013	2016	2017	Average	E_i	Rank	R_i	Rank	
BK-11	12.8	12.6	14.1	13.2	-0.99	3	1.26	2	0.83
BK-13	15.6	15.9	14.3	15.3	1.11	1	-1.22	1	0.98
BK-14	13.3	15.2	15.5	14.7	0.51	2	3.00	3	0.05
BK-19	15.7	15.4	14.1	15.1	0.91	1	-1.77	1	0.48
BK-36	13.7	14.1	15.3	14.4	0.21	2	1.80	3	0.38
BK-37	13.2	13.5	12.8	13.2	-0.99	3	-0.30	1	0.22
BK-52	13.9	14.3	15.5	14.6	0.41	2	1.80	3	0.38
BK-64	12.9	13.8	14.1	13.6	-0.56	2	1.59	2	0.00
BK-65	13.5	15.1	15.4	14.7	0.51	2	2.58	3	0.02
BK-69	12.6	12.9	13.7	13.1	-1.09	3	1.25	2	0.16
LSD _{0.05}		1.1		0.7	0.68	-	0.70	-	-

inferior to the tabular value of the Cochran test ($G_{0.05} = 0.4450$) in all cases. This indicates sufficient homogeneity of the experimentally determined variances within each group, the random nature of the deviations of empirical data from the regression line, and the reliability of the estimates of palmitate variability obtained in the experiments using the Eberhard–Russell algorithm. Thus, the estimates of the variability of this feature depending on the analyzed experimental complex can be considered reliable.

The genetically determined level of the trait and the nature of its changes with fluctuations in the temperatures of the ripening period were not interconnected and manifested themselves as independent properties of both the common type lines and the mutant lines. In each analyzed group, both lines with similar levels of palmitate content and a different response of this trait to fluctuations in the temperature conditions during ripening as well as lines with different levels of palmitate content and a similar response to temperature fluctuations of this period were identified.

The lines of the first of these types include, in particular, the lines of the usual type B-37 and P-523, lines carrying the sh_1 mutation CS-10 and CS-21, and lines carrying the wx mutation BK-14 and BK-19. The second type of lines in our experiments was represented by the lines of the usual type F-115 and P-523, lines carrying the sh_1 mutation CS-15 and CS-21, and lines carrying the wx mutation BK-13 and BK-37.

However, lines that consistently exhibit high or low levels of palmitate under changing growing conditions have the greatest practical value. According to the results of the assessment of intragroup variability, the lines of the common type F-115 and P-523 belonged to this type of lines together with the carriers of mutation sh_1 CS-13, CS-15, and CS-21 and the carriers of mutations wx BK-13, BK-19, and BK-37.

Lines of this type were also identified in the generalized estimates of the entire experimental complex, which included 30 lines belonging to 3 genetically specific groups. In this case, the low content of palmitate and its stable level over the years were shown by the lines F-115 and P-523, and the lines CS-21, BK-13, and BK-19 showed a consistently high level of the trait.

Thus, in our experiments we obtained experimental evidence for the assumption that it is possible to isolate corn lines that exhibit a consistently high or low level of palmitate content under fluctuating growing conditions.

4. Discussion

The results obtained do not give grounds to link the increase in the content of palmitate in the carriers of wx and sh_1 mutations with the direct biochemical effect of these mutant genes.

It is known that both of them belong to the system of genetic regulation of starch synthesis and control the activity of enzymes that catalyze two different reactions of this process. The mutant sh_1 gene regulates the activity of sucrose synthase (Zhang et al., 2020) and the mutant wx gene regulates the activity of granule-bound starch synthase (Li et al., 2018).

Both of these enzymes are not involved in the process of fatty acid synthesis, which is regulated by other enzyme complexes (Zhuang et al., 2022). Therefore, the assumption that the formation of fatty acids and palmitate, in particular, is regulated by the wx and sh_1 mutant genes seems very unlikely.

Therefore, the possible cause of the increased content of palmitate in the carriers of the mutant sh_1 and wx genes is their spatial linkage to the palmitate-coding locus. The prerequisites for this assumption are created by the experimentally proven localization of all these three genetic factors on chromosome 9 (Coe & Schaeffer, 2005; Yang et al., 2010).

The presence of such linkage explains not only the increased content of palmitate in the carriers of the sh_1 and wx mutations but also the existence of individual lines of this type with the palmitate content close to that in the common maize. The reduced content of palmitate in the mutant lines may be related to the crossover distribution of the sh_1 and wx mutant genes on chromosome 9 with a recessive gene that controls the increased content of palmitate.

The results obtained in our experiments indicate that the palmitate-coding locus of chromosome 9 is not the only genetic factor regulating the content of palmitate. This trait in our experiments was of quantitative nature and its level varied quite widely in different lines with identical allelic states of the *sh₁* and *wx* genes.

There is evidence that palmitate-coding loci in maize are located on at least 8 chromosomes, have different expressivity, interact with each other by different types of non-allelic interactions, and are affected by modifier genes (Yang et al., 2010). In addition, in the carriers of *sh₁* and *wx* mutations, there are no guarantees of homozygosity for all loci of the system of genetic regulation of the trait.

If we take into account the free uncontrolled combination of alleles of palmitate-coding loci that are linked and not linked with *sh₁* and *wx* genes, the genetic basis for variations in the level of the trait in the lines with the identical allelic state of these loci of the endosperm structure becomes quite understandable.

It should be noted that such a system of genetic regulation of the content of palmitate creates fundamental opportunities for enhancing the effect of the palmitate-coding loci of chromosome 9 due to its interaction with palmitate-coding loci located in other chromosomes.

The results obtained showed that although *wx* and *sh₁* mutation carriers are not in all cases reliable genetic sources of increased palmitate content in maize, they should be considered as two promising groups of maize genetic diversity in which such sources can be identified.

Our experimental results indicate that in corn, as in many other crops (Zhang et al., 2015), an increase in the content of palmitate in oil is observed under conditions of higher growing temperatures.

A possible explanation for this fact lies in the specifics of the influence of air temperature on the processes of synthesis and interconversions of fatty acids.

According to modern concepts, palmitic acid not only undergoes esterification and is included in the composition of neutral lipids in natural oils, but is also the initial substrate for the synthesis of C 16:1 monounsaturated acids as well as saturated and unsaturated acids with a longer carbon chain (Bates et al., 2013). It is known that the first reactions that lead to the formation of other fatty acids from palmitate are the desaturation of one of the limiting bonds leading to the production of acids of the palmitate-oleate family as well as the elongation of the carbon skeleton leading to the formation of stearic acid (Carta et al., 2017). The first of these reactions is catalyzed by a specific desaturase and the second by a specific elongase (Zhuang et al., 2022).

It has been shown that the intensity of both of these reactions decreases with an increase in air temperature during the ripening period (Menard et al., 2017), which leads to an increase in the content of palmitate. The results of studies conducted to date suggest that the most likely cause of this effect is the inhibition of the activity of enzymes that catalyze reactions involving palmitic acid (Garba et al., 2017).

The results obtained in our experiments showed that the changes in the content of palmitate with temperature fluctuations during the ripening period in different lines of the experimental complex were not identical. In most lines of the common type and in the lines carrying the *sh₁* and *wx* mutations, the content of palmitate varied greatly over the years. However, within each analyzed group, lines with a fairly stable level of palmitate content even in the conditions of fluctuations of growing temperatures were also identified.

Other authors also showed the possibility of the existence of differences in the norms of reactions of varieties and lines of cultivated plants to unidirectional changes in environmental conditions in terms of the fatty acid composition of the oil and, in particular, its content of palmitate (Hemingway et al., 2015). There is an opinion that, according to the nature of the response to fluctuations in environmental conditions, varieties and lines of cultivated plants can be divided into tolerant and sensitive ones (da Cruz et al., 2010). At the same time, tolerant genotypes experience significantly smaller fluctuations in the trait under changing growing conditions than sensitive ones.

The data obtained by us coincide with the results of the studies of these authors and supplement their conclusions by the fact that the genetically determined level of the

trait and its stability under various growing conditions are independent properties of the line and can be combined. Lines that combine these properties are of the greatest practical importance for expanding the useful genetic diversity of corn in terms of palmitate content in oil.

5. Conclusion

Corn inbred lines - carriers of *sh₁* and *wx* mutations differ from the common type lines in a higher content of palmitate, and one of the probable causes for this is the spatial linkage of *sh₁* and *wx* mutant genes to the palmitate-coding locus in chromosome 9. The content of palmitate in unrelated lines - carriers of one mutation varies depending on the genotype of the line and the norms of its reaction to temperature fluctuations during grain ripening. Some lines showed a significant range of palmitate content variability under different temperature regimes of the ripening period, while other lines had a fairly stable level of the trait under the same conditions. Lines with a stably elevated content of palmitate under contrasting temperature growing conditions were identified.

Acknowledgments

The author expresses his deep gratitude to the staff of the «NASCO» Breeding and Seed-Growing station and its Director Mr. Victor Muzhilko for their help in organizing and conducting field experiments on the cultivation of corn lines used for this study.

References

- Aguirrezabal, L., Martre, P., Pereyra-Irujo, G., Echarte, M. M., & Izquierdo, N. (2015). Improving grain quality: Ecophysiological and modeling tools to develop management and breeding strategies. In V. O. Sadras & D. Calderini (Eds.), *Crop physiology: Applications for genetic improvement and agronomy* (pp. 423–465). Acad. Press-Elsevier. <http://dx.doi.org/10.1016/B978-0-12-417104-6.00017-0>
- Alsajri, F. A., Wijewardana, C., Irby, T., Bellaloui, N., Krutz, L. J., Golden, B., Gao, W., & Reddy, K. R. (2020). Developing functional relationships between temperature and soybean yield and seed quality. *Agronomy Journal*, 112(1), 194–204. <http://dx.doi.org/10.1002/agj2.20034>
- Anai, T., Hoshino, T., Imai, N., & Takagi, Y. (2012). Molecular characterization of two high-palmitic-acid mutant loci induced by X-ray irradiation in soybean. *Breeding Science*, 61(5), 631–638. <http://dx.doi.org/10.1270/jsbbs.61.631>
- Bates, P. D., Stymme, S., & Ohlrogge, J. (2013). Biochemical pathways in seed oil synthesis. *Current Opinion in Plant Biology*, 16(3), 358–364. <http://dx.doi.org/10.1016/j.pbi.2013.02.015>
- Bellaloui, N., Mengistu, A., & Kassem, M. A. (2013). Effect of genetics and environment on fatty acid stability in soybean seed. *Food and Nutrition Sciences*, 4(9A1), 165–175. <http://dx.doi.org/10.4236/fns.2013.49A1024>
- Büyüksolak, Z. N., Aşkın, M. A., Kahramanoğlu, İ., & Okatan, V. (2020). Effects of altitude on the pomological characteristics and chemical properties of ‘Chandler’ walnuts: A case study in Uşak Province. *Acta Agrobotanica*, 73(3), Article 7333. <http://dx.doi.org/10.5586/aa.7333>
- Carta, G., Murru, E., Banni, S., & Manca, C. (2017). Palmitic acid: Physiological role, metabolism and nutritional implications. *Frontiers in Physiology*, 8, Article 902. <http://dx.doi.org/10.3389/fphys.2017.00902>
- Coe, E., & Schaeffer, M. L. (2005). Genetic, physical, maps, and database resources for maize. *Maydica*, 50(3), 285–303.
- Coughlan, R., Moane, S., & Larkin, T. (2022). Variability of essential and nonessential fatty acids of Irish rapeseed oils as an indicator of nutritional quality. *International Journal of Food Science*, 1, 1–10. <http://dx.doi.org/10.1155/2022/7934565>
- da Cruz, R. P., Golombieski, J. I., Bazana, M. T., Carbeira, C., Silveira, T. F., & Silva, L. P. (2010). Alterations in fatty acid composition due to cold exposure at the vegetative stage in rice. *Brazilian Journal of Plant Physiology*, 22(3), 199–207. <http://dx.doi.org/10.1590/S1677-04202010000300007>
- Damude, H. G., & Kinney, A. J. (2008). Enhancing plant seed oils for human nutrition. *Plant Physiology*, 147(3), 962–968. <http://dx.doi.org/10.1104/pp.108.121681>

- Das, S., Chaki, A. K., & Hossain, A. (2019). Breeding and agronomic approaches for the biofortification of zinc in wheat (*Triticum aestivum* L.) to combat zinc deficiency in millions of population: A Bangladesh perspective. *Acta Agrobotanica*, 72, Article 1770. <https://pbsociety.org.pl/journals/index.php/aa/article/view/aa.1770/0>
- Dateandtime.info. (2022, April 21). *Geographic coordinates of Nova Kakhovka, Ukraine*. <https://dateandtime.info/citycoordinates.php?id=699839>
- Dospexkhov, B. A. (2011). *Techniques of field experiment (with the basics of statistical processing of research results)* (6th ed.). Alliance (in Russian).
- Garba, L., Ali, M. S. M., Oslan, S. N., & Rahman, R. N. Z. R. B. A. (2017). Review on fatty acid desaturases and their roles in temperature acclimatization. *Journal of Applied Research*, 17(6), 282–295. <http://dx.doi.org/10.3923/jas.2017.282.295>
- Gurieva, I. A., Ryabchun, V. K., Litun, P. P., Stepanova, V. P., Vakulenko, S. M., Kuzmishina, N. V., Kolomatskaya, V. P., & Belkin, A. A. (2003). *Guidelines of field and laboratory study of maize genetic resources* (2nd ed.). National Center for Plant Genetic Resources of Ukraine. (in Ukrainian).
- Hemingway, J., Eskandari, M., & Raican, I. (2015). Genetic and environmental effects on fatty acid composition in soybeans with potential use in the automotive industry. *Crop Sciences*, 55(2), 658–668. <http://dx.doi.org/10.2135/cropsci2014.06.0425>
- Karacor, K., & Cam, M. (2015). Effects of oleic acid. *Medical Science Discovery*, 2(1), 125–132. <http://dx.doi.org/10.17546/msd.25609>
- Karmakar, G., Ghost, P., & Sharma, B. K. (2017). Chemically modifying vegetable oils to prepare green lubricants. *Lubricants*, 5, Article 44. <http://dx.doi.org/10.3390/lubricants5040044>
- Kenar, J. A., Moser, B. R., & List, G. R. (2017). Naturally occurring fatty acids: Source, chemistry, and uses. In M. U. Ahmad (Ed.), *Fatty acids: Chemistry, synthesis, and applications* (pp. 24–82). AOCS Press-Elsevier-Acad. Press. <http://dx.doi.org/10.1016/B978-0-12-809521-8.00002-7>
- Lee, J.-D., Bilyeu, K. D., & Shannon, J. G. (2008). Genetics and breeding for modified fatty acid profile in soybean seed oil. *Journal Crop Science Biotechnology*, 10(4), 201–210.
- Li, C., Huang, Y., Huang, R., Wu, Y., & Wang, W. (2018). The genetic architecture of amylose biosynthesis in maize. *Plant Biotechnology Journal*, 16(2), 688–695. <http://dx.doi.org/10.1111/pbj.12821>
- Manchini, A., Imperlini, E., Nigro, E., Montagnese, C., Daniele, A., Orru, S., & Buono, P. (2015). Biological and nutritional properties of palm oil and palmitic acid: Effects on health. *Molecules*, 20(9), 17339–17361. <http://dx.doi.org/10.3390/molecules200917339>
- Menard, G. N., Moreno, J. M., Bryan, F. M., Munoz-Azcarate, O., Kelly, A. A., Hassani-Pak, K., Kurup, S., & Eastmond, P. (2017). Genome-wide analysis of fatty acid desaturation and its response to temperature. *Plant Physiology*, 173(3), 1594–1605. <http://dx.doi.org/10.1104/pp.16.01907>
- Merrill, L. I., Pike, O. A., Ogden, L. V., & Dunn, M. L. (2008). Oxidative stability of conventional and high-oleic vegetable oils with added antioxidants. *Journal of American Oil Chemists' Society*, 85(8), 771–776. <http://dx.doi.org/10.1007/s11746-008-1256-4>
- Perez-Vich, B., del Moral, M., Velasco, L., Bushman, B. S., Knapp, S. J., Leon, A., Fernandez-Martinez, J. M., & Berry, S. T. (2016). Molecular basis of the high-palmitic acid trait in sunflower seed oil. *Molecular Breeding*, 36, Article 43. <http://dx.doi.org/10.1007/s11032-016-0462-2>
- Pogodaiklimat. (2022, April 21). *Chronicle of weather in New Kakhovka*. <http://www.pogodaiklimat.ru>
- Pollak, L. M., & Scott, M. P. (2005). Breeding for grain quality traits. *Maydica*, 50(3), 247–257.
- Saini, R. K., Rengasamy, K. R. R., Ko, E.-Y., Kim, J.-T., & Keum, Y.-S. (2020). Diversity in fatty acid composition: An investigation to identify PUFA-rich hybrids for a healthy diet. *Frontiers in Nutrition*, 7, Article 5787610. <http://dx.doi.org/10.3389/fnut.2020.578761>
- Salih, N., & Salimon, J. (2021). A review on eco-friendly green biolubricants from renewable and sustainable plant oil sources. *Biointerface Research in Applied Chemistry*, 11(5), 13303–13327. <http://dx.doi.org/10.33263/BRIAC115.1330313327>
- Sanjeev, P., Chaudhary, D. P., Sreevastava, P., Saha, S., Rajendran, A., Sekhar, J. C., & Chikkapa, G. K. (2014). Comparison of fatty acid profile of specialty maize to normal maize. *Journal of the American Oil Chemists' Society*, 91(6), 1001–1005. <http://dx.doi.org/10.1007/s11746-014-2429-y>
- Shannon, J. C., Garwood, D. L., & Boyer, C. D. (2009). Genetics and physiology of starch development. In J. Be Miller & R. Whistler (Eds.), *Starch chemistry and technology* (3rd ed., pp. 24–82). Academic Press-Elsevier. <http://dx.doi.org/10.1016/B978-0-12-746275-2.00003-3>
- Tymchuk, D. S., Sadovnichenko, I., Tymchuk, N., & Potapenko, H. (2021). Oleic acid glycerides content in the oils of maize endospermic mutants and its dependence on temperature during ripening. *Proceedings of the Latvian Academy of Sciences. Section B*.

- Natural, Exact, and Applied Sciences*, 75(5), 403–410.
<http://dx.doi.org/10.2478/prolas-2021-0059>
- White, P. J., Pollak, L. M., & Duvick, S. (2007). Improving the fatty acid composition of corn oil by using germplasm introgression. *Lipid Technology*, 19(2), 35–38.
<http://dx.doi.org/1002/lite.200600009>
- Wiege, B., Fehling, E., Matthaus, B., & Schmidt, M. (2020). Changes in physical and chemical properties of thermally and oxidatively degraded sunflower oil and palm fat. *Foods*, 9(9), Article 1273. <http://dx.doi.org/10.3390/foods9091273>
- Yang, X., Guo, Y., Yan, J., Zhang, J., Song, T., Rocheford, T., & Li, J.-S. (2010). Major and minor QTL and epistasis contribute to fatty acid compositions and oil concentration in high-oil maize. *Theoretical and Applied Genetics*, 120(3), 665–678.
<http://dx.doi.org/10.1007/s00122-009-1184-1>
- Zhang, J.-L., Zhang, S.-B., Zhang, Y.-P., & Kitajima, K. (2015). Effects of phylogeny and climate on seed oil fatty acid composition across 747 plant species in China. *Industrial Crops and Products*, 63, 1–8. <http://dx.doi.org/10.1016/j.indcrop.2014.10.045>
- Zhang, K., Guo, L., Cheng, W., Liu, B., Li, W., Wang, F., Xu, C., Zhao, X., Ding, Z., Zhang, K., & Li, K. (2020). SH1-dependent maize seed development and starch synthesis via modulating carbohydrate flow and osmotic potential balance. *BMC Plant Biology*, 20(1), Article 264. <http://dx.doi.org/10.1186/s12870-020-02478-1>
- Zhuang, X.-Y., Zhang, Y.-H., Xiao, A.-F., Zhang, A.-H., & Fang, B.-S. (2022). Key enzymes in fatty acid synthesis pathway for bioactive lipid biosynthesis. *Frontiers in Nutrition*, 9, Article 851402. <http://dx.doi.org/10.3389/fnut.2022.851402>