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Evaluation of genotype-environment interactions for non-polar lipids and fatty acids in chickpea (*Cicer arietinum* L.) seeds

L.I. Relina, O.Ye. Vazhenina, L.N. Kobyzeva, R.L. Bohuslavsky, S.H. Ponurenko, V.P. Kolomatska, O.M. Bezuhla, O.H. Suprun, N.K. Ilchenko, L.A. Vecherska

Genotype-environment (G × E) interactions for non-polar lipids and fatty acids were studied in 28 chickpea accessions. The total nonpolar lipid content was determined by Soxhlet procedure; fatty acid profiles were investigated by gas chromatography. There were strong negative correlations between oleic and linoleic acids and between oleic and linolenic acids. The correlation between linoleic and linolenic acids was positive and either strong or moderate. Correlations between the other acids were differently directed and of various strengths. Line Luh 99/11 turned out to be an outlier in relation to the other genotypes due to an unusually high content of stearic acid. Cultivar CDC Jade was an outlier because of too low content of stearic acid and too high content of linoleic acid. Accession UD0502195 was an outlier due to a higher content of palmitic acid. Accessions UD0500022 and UD0502195 were outliers due to the low content of total nonpolar lipids. The variability in the total nonpolar lipid content was not affected by the environment, but the environment contributions to the variability of oleic and linoleic acids were very high. There were only statistically significant differences in the oleic and linoleic acid amounts between the cultivation years. There was a positive correlation between the oleic acid content and the average air temperature during the "anthesis – maturity" period and a negative correlation between the linoleic acid content and the average temperature during this period. There was also a negative correlation between the oleic acid content and precipitation during the "anthesis – maturity" period and a positive correlation between the linoleic acid content and precipitation during this period. The palmitic acid content was the most responsive to environmental changes in cultivar CDC Vanguard and the most resistant in cultivar Krasnokutskiy 123. The stearic acid content was the most sensitive to environmental changes in cultivar ILC 3279 and the most irresponsive in accession UKR001:0502116. As to oleic and linoleic acids, line L 273-18 had the bi (plasticity) and S^2di (stability) values coupled with the corresponding mean contents, meaning that this genotype may be adapted to decreased temperature. The ecovalence values (Wi^2) for the total nonpolar lipids, palmitic, stearic and linolenic acids indicated that these characteristics were little responsive to environmental fluctuations. As to oleic and linoleic acids, Wi^2 values were much higher in many accessions, confirming the variability of these parameters depending on growing conditions. Having the highest Wi^2 values, accession Garbanzo 2 is expected to show high degrees of the G × E interactions for oleic and linoleic acids. S^2di was positively correlated with Wi^2.

Key words: *chickpea, oil, correlation, outlier, vegetation phases, analysis of variance, stability, ecovalence.*

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About the authors:

L.I. Relina – The Plant Production Institute named after V.Ya. Yuriev of the National Academy of Agrarian Sciences of Ukraine, Heroiv Kharkova Ave., 142, Kharkiv, Ukraine, 61060, lianaisaakovna@gmail.com, https://orcid.org/0000-0003-2833-5841

O.H. Suprun – The Plant Production Institute named after V.Ya. Yuriev of the National Academy of Agrarian Sciences of Ukraine, Heroiv Kharkova Ave., 142, Kharkiv, Ukraine, 61060, oleg.suprun@ukr.net, https://orcid.org/0000-0002-7708-093X

R.L. Bohuslavskyi – The Plant Production Institute named after V.Ya. Yuriev of the National Academy of Agrarian Sciences of Ukraine, Heroiv Kharkova Ave., 142, Kharkiv, Ukraine, 61060, boguslavr@meta.ua, https://orcid.org/0000-0003-3145-4788

L.A. Vecherska – The Plant Production Institute named after V.Ya. Yuriev of the National Academy of Agrarian Sciences of Ukraine, Heroiv Kharkova Ave., 142, Kharkiv, Ukraine, 61060, lyudmila_vecherska@ukr.net, https://orcid.org/0000-0003-3513-6701

O.M. Bezuhla – The Plant Production Institute named after V.Ya. Yuriev of the National Academy of Agrarian Sciences of Ukraine, Heroiv Kharkova Ave., 142, Kharkiv, Ukraine, 61060, olgabezuglaya61@gmail.com, https://orcid.org/0000-0002-1458-1630

L.N. Kobyzeva – The Plant Production Institute named after V.Ya. Yuriev of the National Academy of Agrarian Sciences of Ukraine, Heroiv Kharkova Ave., 142, Kharkiv, Ukraine, 61060, l.n.kobyzeva@gmail.com, https://orcid.org/0000-0003-3067-7971
O.Ye. Vazhenina – The Plant Production Institute named after V.Ya. Yuriev of the National Academy of Agrarian Sciences of Ukraine, Heroiv Kharkova Ave., 142, Kharkiv, Ukraine, 61060, vajeninaolga29@gmail.com, https://orcid.org/0000-0001-9471-5987
V.P. Kolomatska – The Plant Production Institute named after V.Ya. Yuriev of the National Academy of Agrarian Sciences of Ukraine, Heroiv Kharkova Ave., 142, Kharkiv, Ukraine, 61060, valeriya.kolom@gmail.com, https://orcid.org/0000-0001-5408-4244
S.H. Ponurenko – The Plant Production Institute named after V.Ya. Yuriev of the National Academy of Agrarian Sciences of Ukraine, Heroiv Kharkova Ave., 142, Kharkiv, Ukraine, 61060, serhii_ponurenko@ukr.net, https://orcid.org/0000-0003-0397-636X
N.K. Ilchenko – The Plant Production Institute named after V.Ya. Yuriev of the National Academy of Agrarian Sciences of Ukraine, Heroiv Kharkova Ave., 142, Kharkiv, Ukraine, 61060, masovianalizy@gmail.com, https://orcid.org/0000-0003-1080-1373

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Introduction

Plants encounter different environmental conditions. Responses to these conditions depend on the genetic make-up of plants. When the same genotype develops in different environments, it can generate a variety of phenotypes. These phenotypic variations are attributed to effects of external conditions on the expression of genes influencing the trait of interest. Genotype – environment (G × E) interactions refer to differences in genotypes' responses to different environments (Falconer, Mackay, 1996). First of all, the yield of a crop is highly influenced by the environment. However, the seed quality is also highly dependent on the environment. Fatty acid profiles are one of the determinants of the seed quality. In addition to their roles in the human and animal health, unsaturated fatty acids (UFAs) affect the shelf lives of products, as they undergo oxidation and hydrolysis reactions, eventually turning rancid. This determinant pertains not only to oilseeds, but also to crops with a relatively low oil yield. The chickpea (*Cicer arietinum* L.) is not an oil crop, but it is considered a source of UFAs, as chickpeas are one of the most commonly consumed pulses. Thus, according to the 2018 FAOSTAT data, the chickpea production amounted to 17,192,188 tons (United Nations Data Retrieval System, 2022). *C. arietinum* is a well studied crop for its nutritional value, including lipids (Wallace et al., 2016). However, a great assortment of chickpea cultivars is available and each of them may have its biochemical peculiarities. It should be noted that G × E interactions are generally seldom explored for biochemical characteristics and, in addition, researchers have focused their efforts on exploring heritability and environmental variability of fatty acid profiles in oil crops, like the common olive, but pulses have been completely neglected in this respect. Previously, we determined fatty acid contents in *kabuli* and *desi* seeds, which are a part of the collection of the National Centre for Plant Genetic Resources of Ukraine (in press). Our next objective was to investigate the G × E interactions for total lipids and major fatty acids in chickpea seeds. To our knowledge, it is the first (pilot) study to investigate G × E interactions for these biochemical features of chickpea seeds.

Methods and Materials

Test accessions

Twenty-eight chickpea accessions from the collection of the National Center for Plant Genetic Resources of Ukraine were studied (17 *kabuli* and 11 *desi*). Accessions that are used or planned to be used in crossings and of interest for the chickpea breeding in the Eastern Forest-Steppe of Ukraine were selected for this study. *C. arietinum* was grown in experimental plots of the Plant Production Institute named after V.Ya. Yuriev of NAAS (eastern forest-steppe of Ukraine; Kharkivska Oblast, Kharkivskyi District; N 49°59'39", E 36°27'09") in compliance with conventional farming techniques. Seeds were harvested in 2018, 2019, and 2020. The hydrothermal coefficient (HTC), an indicator that is commonly used in Ukraine to characterize meteorological conditions, was computed (Selyaninov, 2028). The weather conditions during the chickpea growing period differed greatly in 2018, 2019 and 2020. 2019 with an optimal HTC of 0.63 was favorable for chickpea plants; 2020 (HTC = 1.60) was waterlogged, but precipitation was distributed unevenly; 2018 (HTC = 0.43) had the harshest hydrothermal characteristics (Fig. 1). Relationships between the studied characteristics and temperature/precipitation during the chickpea vegetation phases are discussed below in the Result and Discussion section.

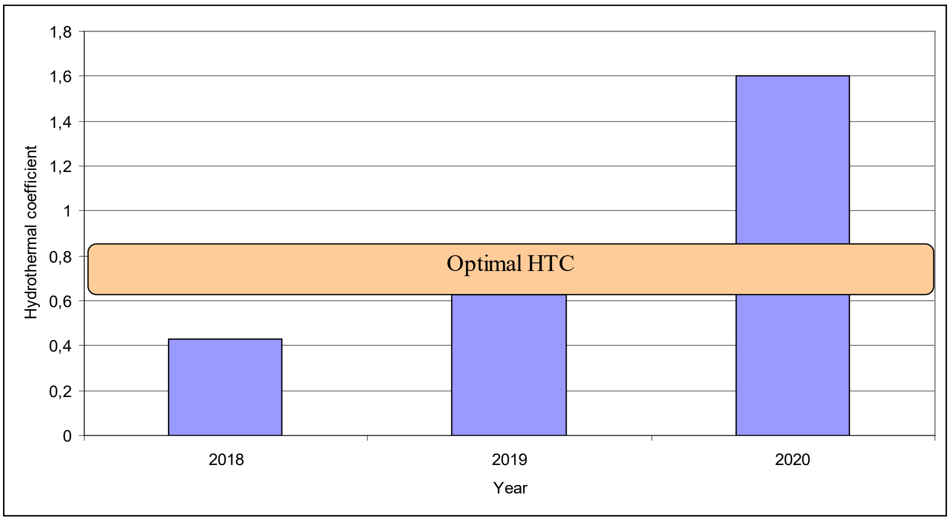

Fig. 1. Meteorological conditions during the chickpea vegetation

Freshly harvested seeds were used for analyses. Whole seeds were milled on a laboratory mill LZM (Olis, LLC, Ukraine). The test accessions were encoded as follows: G1-Rozanna; G2-Dniprovskyi 1; G3-ILC 3279; G4-Kamila 1255; G5-Garbanzo 2; G6-Zehavit; G7-Luh 99/11; G8-Luh 101/11; G9-Alcazaba; G10-UKR001: 0502116; G11-Garbanzo 3; G12-CDC Vanguard; G13-UKR001: 0502059; G14-UKR001: 0502061; G15-Avatar; G16-L 273-18; G17-L 279-18; G18-L 292-18; G19-UD0500196; G20-Chornyi; G21-UD0500022; G22-Krasnokutskiy 123; G23-UKR001: 0501960; G24-UD0502195; G25-Luch; G26-CDC Ebony; G27-CDC Jade; G28-B-90.

Total nonpolar lipid content: Three samples of each accession were analyzed for each year. Lipids were extracted from dried (to the constant weight) whole chickpea seeds (700-800 mg in two replications) by Soxhlet procedure (Juhaimi et al., 2019). Oil was repeatedly washed (percolated) with petroleum ether of boiling range between 40–60°C. The Soxhlet extractor (Cordial, China) was heated to 40°C (hot extraction). After 6-hour incubation at 40°C, the solvent was evaporated under vacuum using a rotary evaporator (Ika, Germany). The percentage of oil in the initial sample was calculated using the following formula:

Total nonpolar lipids (crude oil), % = weight of obtained oil × 100 / weight of absolutely dry milled seeds used in a run.

Gas chromatography: Three samples of each accession were analyzed for each year. Fatty acid methyl esters were prepared by the modified Peisker method (Peisker, 1964). Chloroform-methanol-96% sulfuric acid mixture in a ratio of 100:100:1 was used for methylation. 30–50 μl of lipid extract was placed in a glass ampoule; 2.5 ml of methylation mixture was added, and the ampoule was sealed. Ampoules were incubated in a thermostat at 105°C for 3 hours. After methylation, ampoules were opened, the contents were transferred to test tubes, a pinch of powdered zinc sulfate was added, and then 2 ml of distilled water and 2 ml of hexane were poured to extract methyl esters. After thoroughly stirring and settling, the hexane extracts were filtered and analyzed by gas chromatography (Prokhorova, 1982).

Fatty acid composition was determined using a gas chromatograph Selmikhrom 1 (OAO SELMI, Ukraine) equipped with a flame ionization detector (FID). The stainless steel column, 2.5 m length × 4 mm i.d., was packed with a stationary phase, Inerton AW-DMCS (0.16–0.20 mm) processed with 10% diethylene glycol succinate. 2 μl of hexane solution of fatty acid methyl esters was injected. Gas chromatography was operated under the following conditions: nitrogen flow 30 mL/min; hydrogen flow 30–35 mL/min; air flow 300 mL/min; column temperature 180°C; injector temperature 230°C and FID temperature 220°C. The fatty acids were identified by comparing the retention time of sample with those of reference fatty acid methyl esters (Sigma-Aldrich, US).

Data processing: The percentages of fatty acid methyl esters were calculated by internal normalization. The data were statistically processed in MICROSOFT EXCEL and STATGRAPHICS PLUS. The Mann-Whitney test was used for comparisons. Joint analysis of variance was applied to evaluate the genotype and environmental contributions to the variability. The G × E interactions were assessed using Russell and Eberhart's algorithm (Eberhart, Russell, 1966) and Wricke's ecovalence values (Wricke, 1965), as described in (Ivanenko et al., 1978).

Results and Discussion

We performed correlation analysis for fatty acids in the chickpea. There was a strong negative correlation between oleic and linoleic acids (r=-0.89 – -0.95), which was expected, since in the plant kingdom linoleic acid is synthesized via desaturation (dehydrogenation) of oleic acid (Bernard, 2014; Zhou et al., 2017). There was also a strong negative correlation between oleic and linolenic acids (r=-0.67 – -0.84), and it is known that linoleic acid is dehydrogenated to form linolenic acid (Tanhuanpaa, Schulman, 2002; Timoszuk et al., 2018). The correlation between linoleic and linolenic acids was positive and either strong (r=0.71 in 2019) or moderate (r=0.52 and 0.62 in 2018 and 2020, respectively) in the chickpea accessions under investigation. Oleic acid is synthesized from stearic acid (Benelli et al., 2017), but we observed no significant correlation between these fatty acids in the chickpea. Absence of correlation between oleic and stearic acids was also reported for sunflower (Izquierdo et al., 2006), for *Brassica spp.* and *Brassica rapa* (Stefansson, Storgaard, 1969). There was a moderate negative correlation between oleic and palmitic acids (r=-0.46 – -0.56). Palmitoleic is produced *de novo* by desaturation of palmitic acid (Cahoon, Shanklin, 2000), and we found a moderate positive correlation between these fatty acids (r=0.54–0.60) in the chickpea. Palmitic acid is elongated to stearic acid (Vickery, Vickery, 1981), but there was no significant correlation between these fatty acids. This is generally in line with a study on peanut (a weak correlation was found in one population (Wang et al., 2015), rapeseed and mustard (a significant correlation was only found for *Brassica napus*) (Islam et al., 2009), but it is in disagreement with the findings of Mustiga et al. (2019), who revealed significant negative correlations between the levels of palmitic acid and the downstream fatty acids: stearic (r=-0.74), oleic (r=-0.37), and linoleic acids (r=-0.05) in *Theobroma cacao* L. beans. Eicosanoic acid is produced from stearic acid by elongation (Barker et al., 2007), and the correlation between these fatty acids in the chickpea was positive and either strong (r=0.90 and 0.87 in 2018 and 2019, respectively) or moderate (r=0.52 in 2020).

Thus, relationships between fatty acids may differ not only between species, but even between populations within one species. Such complex patterns are most likely to be due to multiple factors (both genetic and environmental ones) influencing the level of each fatty acid. Taking palmitic acid as an example, one major quantitative trait locus (QTL) and three minor QTLs encoding genes of different isoforms of stearoyl-acyl carrier protein desaturase were located (Zhang et al., 2015) in the chocolate tree. Eleven and 19 QTLs were identified for palmitic acid in two peanut populations (Wang et al., 2015).

The variations in the total lipid and fatty acid contents were low (<10%) or moderate (10–20 %), according to classification of variation ranges (Chepur, 2015) (Fig. 2).

It should be noted that seeds of G7 (Luh 99/11) had an unusually high content of stearic acid. It was statistically proven (ISO 16269-4:2010) that Luh 99/11 was an outlier in relation to the other genotypes (Fig. 3). G27 (CDC Jade) was an outlier because of too low content of stearic acid. In plants, acyl carrier protein (ACP) acts as the acyl carrier for fatty acid synthases (Harwood, 2005). The palmitoyl-ACP is extended by two 2-carbon units to form the stearoyl-ACP by stearoyl-ACP synthase, which is a multienzymatic complex composed of four enzymes (beta-ketoacyl ACP-synthase II, enoyl-ACP reductase, hydroxyacyl-ACP dehydrase, and enoylacyl-ACP reductase) (Harwood, 1996). So, the outlying values can be caused by a mutation in the genes encoding these enzymes or in genes affecting their expression.

There were also outliers for other fatty acids as well as for total nonpolar lipids, though the fluctuations were not as drastic as for stearic acid. CDC Jade was also an outlier for the linoleic acid content. As linoleic acid production is catalyzed by fatty acid desaturase 2 (FAD2) (Bernard, 2014; Zhou et al., 2017), the outlying content of linoleic acid in CDC Jade seeds may be explained by a mutation affecting expression of this enzyme.

G24 (UD0502195) was an outlier because of higher content of palmitic acid. Palmitic acid synthesis is accomplished in the following steps: the beta-ketoacyl-ACP is reduced by beta-ketoacyl-ACP reductase, then dehydrated by beta-hydroxyacyl-ACP dehydratase, and further reduced by enoylacyl-ACP reductase to produce butyryl-ACP. After further condensation with malonyl-ACP, butyryl-ACP is elongated by two C2 units by beta-ketoacyl-ACP synthase I. After seven cycles, palmitoyl-ACP is formed. So, mutations in any of these enzymes can be a cause of the outlying data.

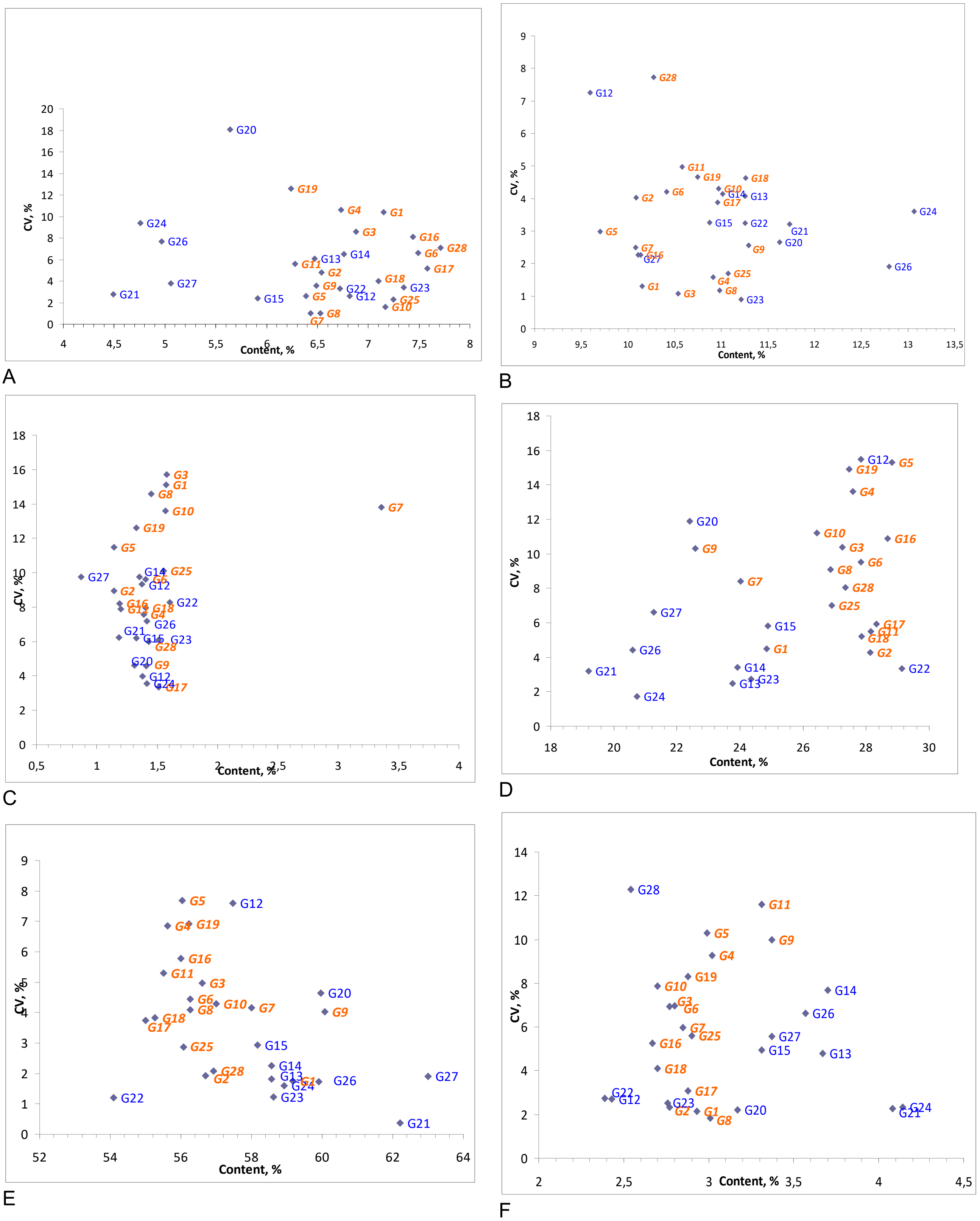

Fig. 2. Mean-CV plots of the crude oil and fatty acid contents. A – total nonpolar lipids; B – palmitic acid; C – stearic acid; D – oleic acid; E – linoleic acid; F – linolenic acid. ***G*** – *kabuli* type, G – *desi* type

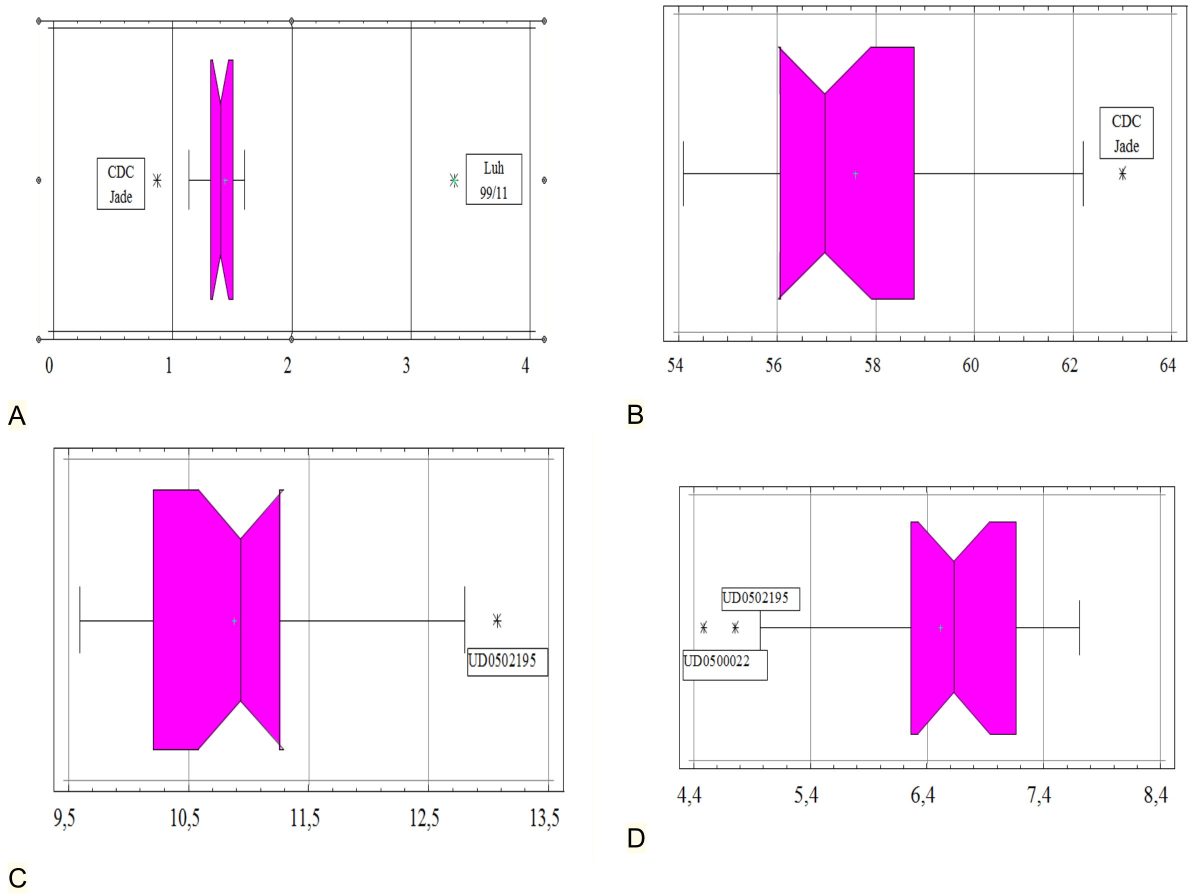

Fig. 3. Box-and whiskers plots of the crude oil and fatty acid contents. A – stearic acid; B – linoleic acid; C – palmitic acid; D – total nonpolar lipids. * – outlier; + – mean; notch – median

G21 (UD0500022) and G24 (UD0502195) were outliers due to a low content of total nonpolar lipids, and there may be a lot of alterations responsible for this peculiarity.

A number of researchers confirmed the high heritability of fatty acid composition (Dabbou et al., 2010; De la Rosa et al., 2016; Ripa et al., 2008; Salimonti et al., 2020). We analyzed the genotype and environmental contributions to the variability of the lipid traits in *C. arietinum* seeds (Table 1).

Table 1. The genotype, environment and G × E interaction contributions to the variability of the total nonpolar lipid and fatty acid contents in *C. arietinum* seeds (% of total)

Trait	Genotype	Environment	G × E interaction
Total nonpolar lipid content	84.68	1.17	14.16
Palmitic acid content	82.90	4.49	12.17
Stearic acid content	89.99	0.05	9.97
Oleic acid content	63.3	10.50	26.09
Linoleic acid content	48.73	20.46	30.83
Linolenic acid content	87.69	1.53	10.87

Thus, the variability in the total nonpolar lipid content was not affected by the environment. The environment did not contribute to the variability of the stearic acid content either. The environment contributions to the variability of the palmitic and linolenic acid contents were statistically significant, but low; that is why we observed not significant differences in these fatty acids between the cultivation years. As to oleic and linoleic acids, the environment contributions to their variability were much higher, which is generally in agreement with other researchers' data (see below). The 'genotype-environment' interaction effects were also the most pronounced for oleic and linoleic acids.

We detected no significant differences in the palmitic or stearic acid levels, i.e. major saturated acids, between the growing conditions (cultivation years). Brock et al. (2020) also showed that saturated (but not unsaturated) fatty acid accumulation was unaffected by environment in gold-of-pleasure. Nevertheless, many authors reported that increased temperature contributed to a rise in palmitic acid content (Falcone et al., 2004; Lehrian et al., 1980; Mustiga et al., 2019; Liu, Huang, 2004; Wintgens, 1992). Martínez-Force et al. (1998) found that all mutant (high-stearic and high-palmitic) sunflower lines increased palmitic acid content at high growth temperature and almost all mutants increased stearic acid content at low temperature, though one could expect a decline in all saturated fatty acids, including stearic, as a result of a temperature drop. Rainfall and sunlight were also shown to affect the palmitic acid level (Mustiga et al., 2019; Shen et al., 2018).

In our study, there were only statistically significant differences in the oleic and linoleic amounts between the cultivation years (Fig. 4).

The oleic acid level was lower both in the *kabuli* and in *desi* accessions in 2020 and in 2018 than in 2019. The 2018 and 2020 years differed for the *kabuli* types only: the oleic acid content in *kabuli* seeds was higher in 2018 than in 2020. An opposite trend was observed for linoleic acid: its content was higher both in the *kabuli* and in *desi* accessions in 2020 and in 2018 than in 2019. The linoleic acid content was higher in 2020 than in 2018. Such opposite changes seem to be quite logical, as in the plant kingdom linoleic acid is synthesized via desaturation of oleic acid by FAD2 (Bernard, 2014; Zhou et al., 2017).

We analyzed these differences in the context of temperature and rainfall during different phases of chickpea plant development. No consistent patterns were observed between the linoleic and oleic acids contents and air temperature or precipitation amount during the "sowing-emergence" and "emergence-anthesis" periods. However, there was a strong or moderate positive correlation between the oleic acid content and the average air temperature during the "anthesis – maturity" period ($r=0.84$ ($P<0.05$) and $r=0.60$ ($P<0.05$) for the *kabuli* and *desi* types, respectively). Concurrently, there was a strong or moderate negative correlation between the linoleic acid content and the average temperature during this period ($r=-0.84$ ($P<0.05$) and $r=-0.70$ ($P<0.05$) for the *kabuli* and *desi* types, respectively). This is in line with data obtained on other crops. FAD2 activity depends on temperature in sunflower (Martínez-Rivas et al., 2000) FAD2 genes are known to play the direct role in adaptation to cold stress in different plant species (Dar et al., 2017), including cotton (Kargiotidou et al., 2008), arabidopsis (Maeda et al., 2008), common olive (Matteucci et al., 2011) and in soybean (Byfield, Upchurch, 2007). A FAD2-2 isoform was shown to be involved in the response to drought in common olive (Hernández et al., 2009, 2018). Levels of other unsaturated fatty acids also tend to increase during cold adaptation. Soybean oil accumulated more linolenic acid when plants were cultivated at a decreased temperature (Lanna et al., 2005). Liu et al. (2019) hypothesized that palmitoleic acid may play an important role in developing upland cotton seeds, especially under cold stress.

We also found a strong negative correlation between the oleic acid content and the precipitation amount during the "anthesis – maturity" period ($r=-0.95$ ($P<0.05$) and $r=-0.98$ ($P<0.05$) for the *kabuli* and *desi* types, respectively). In parallel, there was a strong positive correlation between the linoleic acid content and the precipitation amount during this period ($r=0.95$ ($P<0.05$) and $r=0.98$ ($P<0.05$) for the *kabuli* and *desi* types, respectively). These results are consistent with data reported for other crops. Water deficit caused a decrease in the linoleic acid content in olive mesocarp. Analysis of the fatty acid composition in water-deficient stressed *Brassica napus* showed decreased contents of linoleic and linolenic acids in phospholipid fractions (Dakhma et al., 1995). Mekki et al. (1999) reported that drought stress increased the percentage of palmitic acid. Water deficit stress also increased the stearic acid content in canola cultivars (Moghadam et al., 2011).

The discrepancies between data of different authors and our data concerning saturated fatty acids and palmitoleic or linolenic fatty acids can be explained by different stages of ontogenesis under investigation or by different solvents used for lipid extraction. Petroleum ether extracts mainly nonpolar lipids (triglycerides), while membrane lipids are amphiphilic, and mixtures for their extraction are to contain polar solvents (with methanol being the most common one). At the same time, it is membrane lipids that are supposed to respond to environmental changes (primarily to temperature). When temperature drops, the composition of membrane lipids tends to become more unsaturated to maintain homeoviscosity. Thus, the levels of petroleum ether-extracted lipids may not change in parallel with environment-induced general patterns in fatty acid composition. Further research is needed to elucidate if there are any relationships between fatty acid profiles in membrane lipids from plants vegetating under different environmental conditions and in lipids from mature seeds.

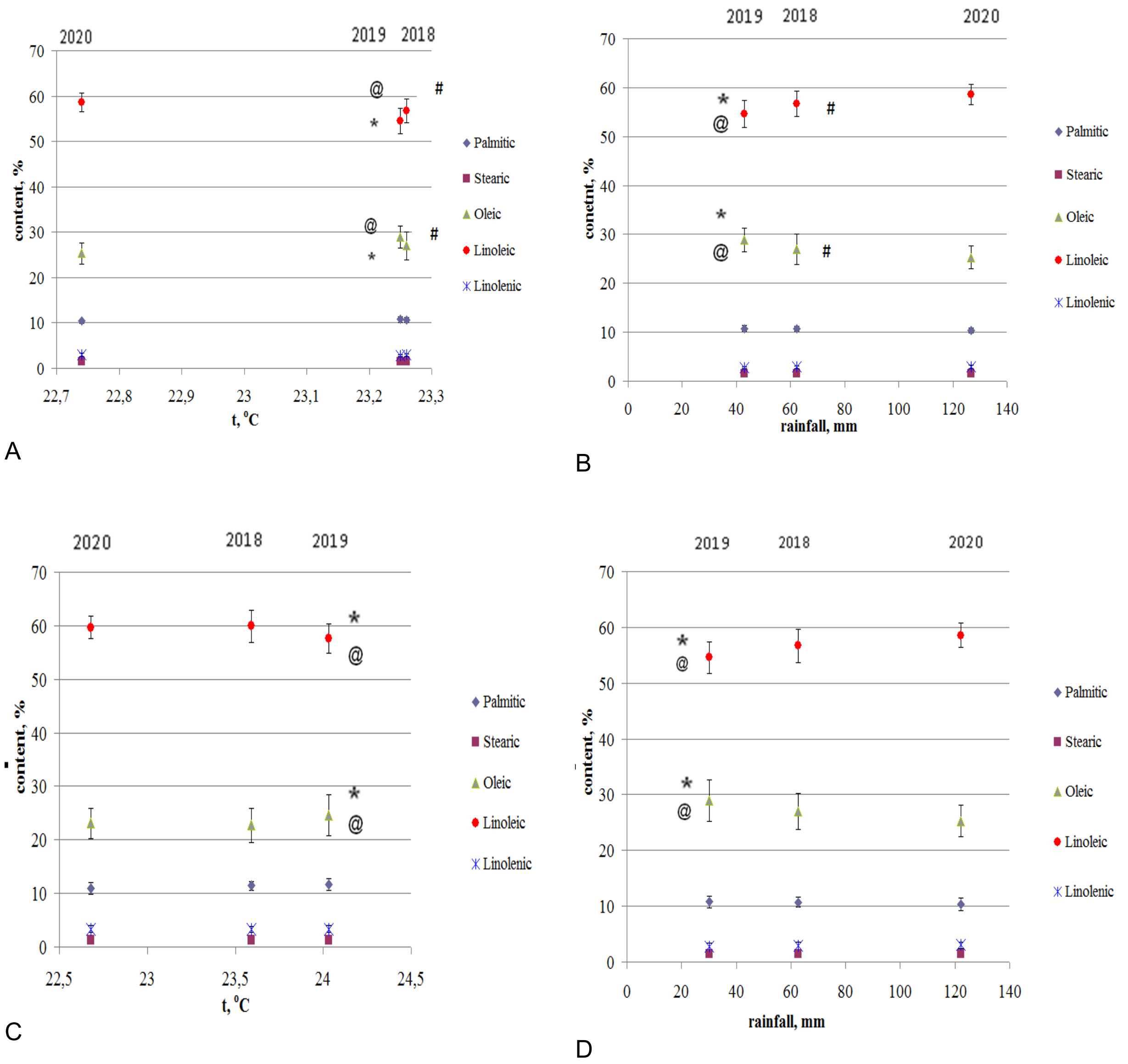

Fig. 4. Plots of the mean contents of fatty acids versus average temperature and precipitation amount during the “anthesis – maturity” period. A, B – *kabuli* type; C, D – *desi* type. * – significant difference between 2019 and 2020; @ – significant difference between 2019 and 2018: # – significant difference between 2018 and 2020

To analyze how the chickpea accessions respond to environmental changes, we applied Russell and Eberhart’s algorithm (Fig. 5). A wide adaptability genotype is defined as one with bi=1 and high stability as one with S^2di=0. Here, we should emphasize that Russell and Eberhart’s method is usually used to evaluate yield/performance, so high and stable yields are sure to be recognized as promising ones (Lule et al., 2014). However, when discussing biochemical parameters, interpretation may differ. For example, high stability of linoleic content may be beneficial with regard to seed quality and nutritional value, but detrimental to plants in the context of adaptation to heat stress.

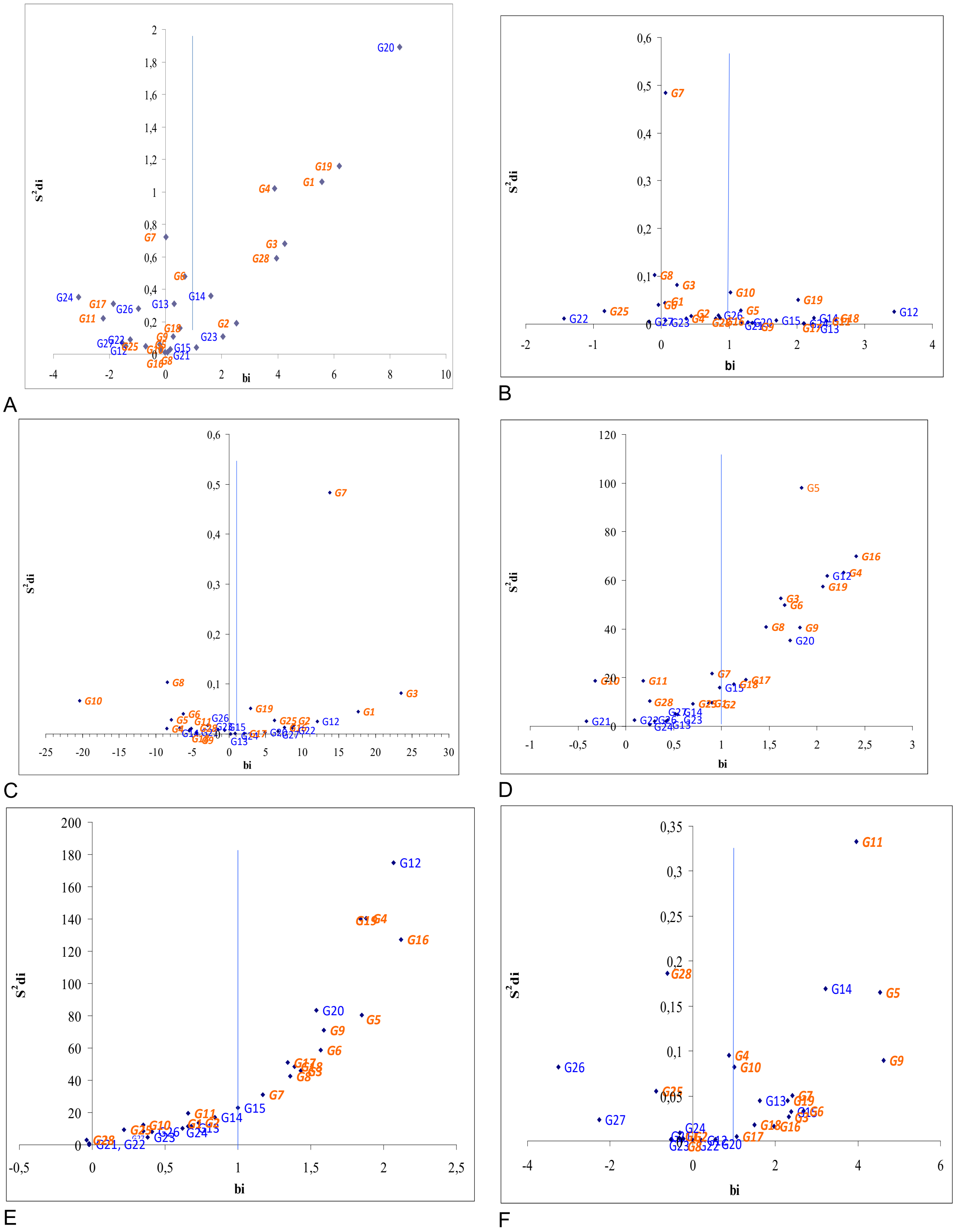

Fig. 5. Biplot for regression coefficient (bi) and deviation from regression (S^{2}di) stability parameters. A – total nonpolar lipids; B – palmitic acid; C – stearic acid; D – oleic acid; E – linoleic acid; F – linolenic acid. ***G*** – *kabuli* type, G – *desi* type

Table 2. Wricke's ecovalence for the total nonpolar lipid and fatty acid contents in chickpea seeds

Genotype	Total lipids	Palmitic	Stearic	Oleic	Linoleic	Linolenic
G1	0.80	0.11	0.13	0.09	0.64	0.02
G2	0.08	0.42	0.02	0.39	0.41	0.02
G3	0.47	0.08	0.13	10.92	9.20	0.02
G4	0.81	0.10	0.02	21.10	21.31	0.16
G5	0.10	0.07	0.03	37.63	31.14	0.15
G6	0.48	0.58	0.05	8.28	3.75	0.03
G7	0.04	0.24	0.53	6.99	7.06	0.03
G8	0.03	0.16	0.11	7.16	3.93	0.02
G9	0.12	0.03	0.01	2.99	2.42	0.19
G10	0.07	0.44	0.12	28.33	16.51	0.08
G11	0.41	0.30	0.02	20.35	19.97	0.28
G12	0.17	0.61	0.03	33.48	30.03	0.01
G13	0.32	0.16	0.00	1.29	0.62	0.03
G14	0.32	0.16	0.04	1.27	0.47	0.13
G15	0.00	0.05	0.01	1.34	1.60	0.02
G16	0.75	0.05	0.01	9.17	7.88	0.01
G17	0.45	0.12	0.00	0.92	1.07	0.00
G18	0.16	0.26	0.03	0.20	1.17	0.00
G19	0.89	0.31	0.06	29.39	23.20	0.10
G20	1.62	0.07	0.00	8.12	7.80	0.00
G21	0.05	0.17	0.01	8.19	5.79	0.03
G22	0.20	0.71	0.03	5.60	6.69	0.01
G23	0.03	0.11	0.01	1.73	2.42	0.03
G24	0.61	0.21	0.00	2.25	0.81	0.03
G25	0.13	0.35	0.06	7.28	9.27	0.09
G26	0.38	0.04	0.02	3.61	3.66	0.20
G27	0.20	0.24	0.01	4.77	5.28	0.14
G28	0.40	1.48	0.01	14.12	9.35	0.26

The total nonpolar lipid content was the most sensitive to environmental changes in G20 (Choprnyi) and the most resistant in G24 (UD0502195), with S^2di values not significantly different from zero. The palmitic acid content was the most sensitive to environmental changes in G12 (CDC Vanguard) and the most resistant in G22 (Krasnokutskiy 123), with very low values of S^2di, too. The other accessions also had very low values of S^2di, though with bi closer to 1. Thus, CDC Vanguard is adapted to environments favoring high levels of palmitic acid (which may reflect adaptation to increased temperature), while Krasnokutskiy 123, vise versa, may be adapted to cool environments. It is noteworthy that the assumption about Krasnokutskiy 123 was confirmed by multi-year field surveys, which showed that this cultivar better survived during cool periods than other accessions. Similar considerations can be applied to stearic acid, though different genotypes stood out with marginal values. The stearic acid content was the most sensitive to environmental changes in G3 (ILC 3279) and the most resistant in G10 (UKR001: 0502116), with very low values of S^2di. It should be noted that G7 (Luh 99/11) had the highest S^2di values for palmitic and stearic acids, though they were not significantly different from zero, either. As to the oleic and linoleic acid contents, the patterns were different. S^2di values for oleic and linoleic acids were much higher than for saturated ones. For example, for oleic acid, G16 (L 273-18) and G5 (Garbanzo 2) had bi of 2.41 and 1.84 and S^2di of 70.0 and 98.1 coupled with the mean content of 28.6% and 28.8%, respectively, meaning that these genotypes may be adapted to decreased temperature. As for linoleic acid, G12 (CDC Vanguard) and G4 (Kamila 1255) had the highest values of S^2di: 174.8 and 140.3, respectively, (bi of 2.07 and 1.88), with the mean content of 57.5% and 55.6%, respectively. G16 (L 273-18) and G19 (UD0500196) also had fairly high values of bi and S^2di: 2.12 and 1.84, respectively, and 127.3 and 139.9, respectively. The mean content of linoleic content in seeds of these chickpea accessions was 56.0% and 56.2%, respectively. Hence, much greater variability is intrinsic to oleic and linoleic acids in chickpea seeds as compared to other fatty acids, which may be a consequence of membrane adaptability to temperature fluctuations. L 273-18, Garbanzo 2, CDC Vanguard, Kamila 1255, and UD0500196 were later acquired by the National Center for Plant Genetic Resources of Ukraine and have not been yet tested for survival at decreased temperature. We suppose that they can be adaptable to cool weather too, like Krasnokutskiy 123, but this supposition needs further verification in the field. However, no clear patterns were observed for linolenic acid, which had near zero S^2di values and bi ranging from -3.25 (G26; CDC Ebony) to 4.62 (G9; Alcazaba).

The ecovalence (Wi^2) is a measure of the G × E interaction. Wi^2 is equal to zero (or near zero) if there is no (or negligible) G × E interaction. The Wricke's ecovalence values for the total nonpolar lipids, palmitic, stearic and linolenic acids were generally in line with our conclusions on these characteristics drawn from the other evaluation approaches: these parameters are little responsive to environmental changes (Table 2). The S^2di-Wi^2 correlation coefficients amounted to 0.96, 0.67, 0.98, 0.69, 0.63, and 0.85 for total lipids, palmitic, stearic, oleic, linoleic, and linolenic acids, respectively. As to oleic and linoleic acids, Wi^2 were much higher in many accessions, confirming the variability of these parameters depending on growing conditions. G5 (Garbanzo 2) had the highest Wi^2 values for the oleic and linoleic acid contents, attesting to high degrees of the G × E interaction for these characteristics, which was in agreement with the assessment by Russell and Eberhart's method. G12 (CDC Vanguard) had the second highest value of Wi^2 for linoleic acid, which also agreed with the assessment by Russell and Eberhart's method. However, there were some discrepancies for other genotypes: G12 (CDC Vanguard), G19 (UD0500196) and G10 (UKR001: 0502116) (not G16 (L 273-18)) had the second, third and fourth highest values of Wi^2 for oleic acid.

Conclusions

Correlation analysis revealed differently directed correlations of various strengths between fatty acids in the chickpea accessions under investigation. The variations in the total lipid and fatty acid contents were low or moderate. Seeds of Luh 99/11 had an unusually high content of stearic acid, making this genotype an outlier in relation to the other genotypes. CDC Jade was an outlier because of too low content of stearic acid. CDC Jade was also an outlier for the linoleic acid content. UD0502195 was an outlier because of higher content of palmitic acid. UD0500022 and UD0502195 were outliers due to the low content of total nonpolar lipids. The variability in the total nonpolar lipid content was not affected by the environment. The environment did not contribute to the variability of the stearic acid content either. As to oleic and linoleic acids, the environment contributions to their variability were much higher. There were only statistically significant differences in the oleic and linoleic acid amounts between the cultivation years. There was a positive correlation between the oleic acid content and the average air temperature during the "anthesis – maturity" period and a negative correlation between the linoleic acid content and the average temperature during this period. We also found a negative correlation between the oleic acid content and the precipitation amount during the "anthesis – maturity" period and a positive correlation between the linoleic acid content and the precipitation amount during this period. The palmitic acid content was the most sensitive to environmental changes in CDC Vanguard and the most resistant in Krasnokutskiy 123. Thus, CDC Vanguard may be adapted to environments with increased temperature favoring high levels of palmitic acid, while Krasnokutskiy 123, vise versa, may be adapted to cool environments. The stearic acid content was the most sensitive to environmental changes in ILC 3279 and the most resistant in UKR001: 0502116. For oleic and linoleic acids, L 273-18 had the bi and S^2di values coupled with the corresponding mean contents, meaning that this genotype may be adapted to decreased temperature. The Wricke's ecovalence values for the total nonpolar lipids, palmitic, stearic and linolenic acids indicated that these characteristics were hardly responsive to environmental changes. As to oleic and linoleic acids, Wi^2 values were much higher in many accessions, confirming the variability of these parameters depending on growing conditions. Having the highest Wi^2 values, Garbanzo 2 is expected to show high degrees of the G × E interactions for oleic and linoleic acids.

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Оцінка взаємодії генотип-середовище за ознаками вмісту неполярних ліпідів та жирних кислот в насінні нуту (*Cicer arietinum* L.)

Л.І. Реліна, О.Є. Важеніна, Л.Н. Кобизєва, Р.Л. Богуславський, С.Г. Понуренко,
В.П. Коломацька, О.М. Безугла, О.Г. Супрун, Н.К. Ільченко, Л.А. Вечерська

Взаємодії генотип-середовище (Г × С) за ознаками вмісту неполярних ліпідів та жирних кислот вивчались в 28 зразках нуту. Загальний вміст неполярних ліпідів визначали за методикою Сокслета; жирнокислотний склад вивчали методом газової хроматографії. Встановлено сильні негативні кореляції між вмістом олеїнової та лінолевої кислот, а також між вмістом олеїнової та ліноленової кислот. Кореляція між вмістом лінолевої та ліноленової кислот була позитивною і сильною або помірною. Кореляції між іншими кислотами характеризувались різнонаправленістю та були різної сили. Лінія Луг 99/11 виявилась викидом по відношенню до інших генотипів через незвичайно високий вміст стеаринової кислоти. Сорт CDC Jade був викидом через надзвичайно низький вміст стеаринової кислоти та надзвичайно високий вміст лінолевої кислоти. Зразок UD0502195 був викидом через підвищений вміст пальмітинової кислоти. Зразки UD0500022 та UD0502195 були викидами через низький загальний вміст неполярних ліпідів. Навколишнє середовище не впливало на варіабельність загального вмісту неполярних ліпідів, проте внески середовища в варіабельність вмісту олеїнової та лінолевої кислот були дуже високими. Відмінності між роками вирощування були статистично значущими тільки для олеїнової та лінолевої кислот. Встановлено позитивну кореляцію між вмістом олеїнової кислоти та середньою температурою повітря в період “цвітіння – зрілість” і негативну кореляцію між вмістом лінолевої кислоти та середньою температурою за цей період. Також встановлено негативну кореляцію між вмістом олеїнової кислоти та сумою опадів в період “цвітіння – зрілість” і позитивну кореляцію між вмістом лінолевої кислоти та сумою опадів за цей період. Вміст пальмітинової кислоти був найбільш чутливим до змін навколишнього середовища в насінні сорту CDC Vanguard і найбільш стійким в насінні сорту Краснокутський 123. Вміст стеаринової кислоти був найбільш чутливим до змін навколишнього середовища в насінні сорту ILC 3279 і найбільш стійким в насінні зразка UKR001:0502116. Що стосується олеїнової та лінолевої кислот, лінія Л 273-18 характеризувалась значеннями bi та S^2di, які у поєднанні з відповідними середніми значеннями вмісту, означають, що цей генотип може адаптуватись до знижених температур. Значення еквалентності (Wi^2) за ознаками загальний вміст неполярних ліпідів, вміст пальмітинової, стеаринової і ліноленової кислот вказували на те, що ці характеристики слабо реагували на коливання навколишніх умов. Щодо олеїнової та лінолевої кислот, значення Wi^2 були набагато вищі у багатьох зразках, що підтверджує варіабельність цих параметрів в залежності від умов вирощування. Оскільки зразок Garbanzo 2 мав найвищі значення Wi^2, можна очікувати, що йому будуть притаманні високі ступені взаємодій Г × С за ознаками олеїнової та лінолевої кислот.

Ключові слова: *нут, олія, кореляція, викид, фази вегетації, дисперсійний аналіз, стабільність, ековалентність.*

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Про авторів:
Л.І. Реліна – Інститут рослинництва ім. В.Я. Юр’єва Національної академії аграрних наук України, пр. Героїв Харкова, 142, Харків, Україна, 61060, lianaisaakovna@gmail.com, https://orcid.org/0000-0003-2833-5841
О.Г. Супрун – Інститут рослинництва ім. В.Я. Юр’єва Національної академії аграрних наук України, пр. Героїв Харкова, 142, Харків, Україна, 61060, oleg.suprun@ukr.net, https://orcid.org/0000-0002-7708-093X
Р.Л. Богуславський – Інститут рослинництва ім. В.Я. Юр’єва Національної академії аграрних наук України, пр. Героїв Харкова, 142, Харків, Україна, 61060, boguslavr@meta.ua, https://orcid.org/0000-0003-3145-4788
Л.А. Вечерська – Інститут рослинництва ім. В.Я. Юр’єва Національної академії аграрних наук України, пр. Героїв Харкова, 142, Харків, Україна, 61060, lyudmila_vecherska@ukr.net, https://orcid.org/0000-0003-3513-6701
О.М. Безугла – Інститут рослинництва ім. В.Я. Юр’єва Національної академії аграрних наук України, пр. Героїв Харкова, 142, Харків, Україна, 61060, olgabezuglaya61@gmail.com, https://orcid.org/0000-0002-1458-1630
Л.Н. Кобизєва – Інститут рослинництва ім. В.Я. Юр’єва Національної академії аграрних наук України, пр. Героїв Харкова, 142, Харків, Україна, 61060, l.n.kobyzeva@gmail.com, https://orcid.org/0000-0003-3067-7971
О.Є. Важенина – Інститут рослинництва ім. В.Я. Юр’єва Національної академії аграрних наук України, пр. Героїв Харкова, 142, Харків, Україна, 61060, vajeninaolga29@gmail.com, https://orcid.org/0000-0001-9471-5987
В.П. Коломацька – Інститут рослинництва ім. В.Я. Юр’єва Національної академії аграрних наук України, пр. Героїв Харкова, 142, Харків, Україна, 61060, valeriya.kolom@gmail.com, https://orcid.org/0000-0001-5408-4244
С.Г. Понуренко – Інститут рослинництва ім. В.Я. Юр’єва Національної академії аграрних наук України, пр. Героїв Харкова, 142, Харків, Україна, 61060, serhii_ponurenko@ukr.net, https://orcid.org/0000-0003-0397-636X
Н.К. Ільченко – Інститут рослинництва ім. В.Я. Юр’єва Національної академії аграрних наук України, пр. Героїв Харкова, 142, Харків, Україна, 61060, masovianalizy@gmail.com, https://orcid.org/0000-0003-1080-1373

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