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Original article

Assessment of Combining Ability of Sunflower Lines Resistant to Sulfonylurea Herbicides in the Southern Steppe of Ukraine

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Abstract

To develop competitive sunflower hybrids, a sufficient number of parental components with agronomically valuable traits and a high level of combining ability is required. This study determined the general and specific combining ability of 40 inbred sunflower lines from the breeding programme of The Plant Breeding and Genetics Institute - National Center of Seed and Cultivar Investigation (Ukraine) that are resistant to sulfonylurea herbicides, with respect to seed yield under unstable moisture conditions in the Southern Steppe of Ukraine. The goal was to identify water-stress-adapted donors and to form highly productive hybrid combinations. Combining ability was evaluated in 2020–2023 for the trait "seed yield". Significant variability in general and specific combining ability was observed depending on hydrothermal conditions and genotype. Statistical analysis of seed yield identified seven lines that consistently showed high combining ability and can be recommended for further breeding studies.

Keywords: Sunflower, Combining Ability, Inbred Lines, Seed Yield

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INTRODUCTION

Sunflower is the fourth most important oilseed crop in the world after soybeans, peanuts, and rapeseed, and it is one of the most widely grown crops in Ukraine, accounting for about one-fifth of the country's crop area. In 2021, Ukraine harvested a record 16.4 million tons of sunflower seed (about 31% of global production). The full-scale Russian invasion in 2022 significantly affected the sown area and the total sunflower harvest in Ukraine. The total sown area decreased from 6.6 million hectares in 2021 to 4.8 million hectares (Qadir, Skakun, Becker-Reshef, Kussul, & Shelestov, 2024; Shevchenko, Petrenko, & Gelas, 2024). Despite the difficult situation in agro-industrial production and unfavourable weather conditions, Ukraine continues to grow sunflower on large areas and achieve high yields. According to the Ministry of Agrarian Policy and Food of Ukraine, as of 2024, 10.2 million tons of seed were obtained from 4.9 million hectares. To increase seed yield, breeders continuously develop new inbred lines and hybrids and improve agronomic practices. However, seed yield is influenced by many external factors, including disease pressure, pest damage, and adaptation to unfavourable environmental conditions.

In agricultural production, it is important to select hybrids that are adapted to local conditions and provide high and stable yields. Climatic conditions in Ukraine range from sufficiently humid in the western Forest-Steppe to extremely dry in the southern Steppe. Based on the water balance coefficient, two moisture zones are distinguished in Ukraine: unstable (coefficient close to 1) and insufficient (coefficient < 1). In Odesa, Mykolaiv, and Kherson regions, the water balance coefficient ranges from 0.50 to 0.68, which characterises them as zones of insufficient moisture (Kobzar & Osadchyi, 2018).

In the Southern Steppe of Ukraine, the main focus of sunflower breeding is the development of high-yielding mid-early and mid-maturing hybrids with 52–54% oil content, resistant to heat, drought, broomrape, and downy mildew (Sydiakina & Podriezov, 2024). One of the key tasks of modern sunflower breeding is to improve the effectiveness of weed control in arid regions of Ukraine. Conventional agronomic measures do not always ensure stable weed control, especially under unstable moisture conditions in the Southern Steppe. Therefore, marker-assisted selection (MAS) is widely used in breeding programmes to identify and select genotypes carrying alleles that confer resistance to sulfonylurea herbicides. MAS can substantially accelerate the development of new inbred lines and sunflower hybrids by combining conventional breeding with modern biotechnological approaches (Kucherenko et al., 2022).

Combining ability is an important indicator of source material in heterosis breeding. This trait is genetically determined and is expressed under self-pollination and across different growing conditions (Khan, Swati, Khalil, & Iqbal, 2003). The concept of "combining ability" was introduced by G. F. Sprague and L. A. Tatum, who distinguished general combining ability (GCA) and specific combining ability (SCA) (Sprague & Tatum, 1942). Effective hybrid selection depends on choosing parental components with high GCA and SCA values (Zhang, Li, Wang, Liu, & Sun, 2021). GCA reflects the average performance of a line across combinations and mainly represents additive gene effects, whereas SCA reflects non-additive effects, including dominance and epistasis (Kaya & Atakisi, 2004).

Evaluating crop genotypes using GCA and SCA effects, the ratio of their variances in the first hybrid generation, and the type of gene action (additive or non-additive) is important for predicting the expression of breeding traits, assessing selection efficiency in hybrid populations for quantitative traits, and substantiating breeding strategies (Fasahat, Rajabi, Rad, & Derera, 2016).

The success of heterosis sunflower breeding significantly depends on the creation, selection and evaluation of parental lines (forms). When creating high-yielding sunflower hybrids, the key objective is to identify components capable of providing high heterosis effects when crossbreeding. This is achieved by combining three main methodological approaches: inbreeding, combining ability assessment of inbred lines and selection of parental components in accordance with their high level of combining ability (Ibitome, 2010).

Previous studies have shown that lines with high values of the GCA effects provide stable hybrid productivity regardless of the crossing combination (Gundaev, 2018). However, certain hybrid combinations may demonstrate increased productivity due to high variances of SCA (Volf, Dumacheva, & Kiryushin, 2017).

The aim of this study was to determine the general and specific combining ability of inbred sunflower lines resistant to sulfonylurea herbicides, with respect to seed yield under unstable moisture conditions in the Southern Steppe of Ukraine, in order to identify donors adapted to water stress and to develop highly productive hybrid combinations.

MATERIALS AND METHODS

The research was conducted in the scientific crop-rotation fields of The Plant Breeding and Genetics Institute - National Center of Seed and Cultivar Investigation, located in a zone of unstable moisture, at the Department of Breeding and Seed Production of Cross-Pollinated Crops. Field experiments were carried out during 2020–2023 near the village of Dachne, Odesa region (Odesa oblast, Ukraine; 46.574043, 30.536585).

The study included 40 inbred sunflower lines resistant to sulfonylurea herbicides: OSU 1511 R, OSU 1512 R, OSU 1513 R, OSU 1514 R, OSU 1515 R, OSU 1516 R, OSU 1517 R, OSU 1518 R, OSU 1519 R, OSU 1520 R, OSU 1521 R, OSU 1522 R, OSU 1523 R, OSU 1524 R, OSU 1526 R, OSU 1527 R, OSU 1529 R, OSU 1530 R, OSU 1532 R, OSU 1533 R, OSU 1534 R, OSU 1535 R, OSU 1536 R, OSU 1537 R, OSU 1538 R, OSU 1539 R, OSU 1540 R, OSU 1541 R, OSU 1543 R, OSU 1544 R, OSU 1546 R, OSU 1547 R, OSU 1548 R, OSU 1549 R, OSU 1551 R, OSU 1552 R, OSU 1553 R, OSU 1554 R, OSU 1556 R, and OSU 1566 R (Ilchenko, Varenyk, & Karapira, 2024). The lines were developed using hybrids and lines of domestic and foreign breeding maintained and multiplied in collection nurseries, including SURES-1 and SURES-2, which served as donors of sulfonylurea herbicide resistance. At all stages of line development, marker-assisted selection was used, specifically DNA-based identification of the mutant allele of the *AHAS1* gene (Solodenko & Fayt, 2018). Lines adapted to the Southern Steppe of Ukraine, resistant to a complex of diseases and pests, and characterised by increased seed yield, plasticity, and the ability to realise their genetic potential under different growing conditions were selected.

Hybridisation was carried out to the tester crossing scheme (Griffing, 1956; Litun, Kyrychenko, Petrenkova, & Kolomatska, 2009). To obtain hybrids, the studied lines were crossed with the tester lines: Od 1002 A, Od 1008 A and Od 1042 A.

The resulting hybrids were sown with a HEGE 95 pneumatic precision planter in the third decade of April. The experiment was conducted in three replicates. Plot area was 20 m^2, and the harvest (accounting) area was 10 m^2. Plant density was 50–55 thousand plants per hectare. Field observations and measurements were performed during the growing season. After maturity, hybrids from the accounting plots were harvested using a Sampo-130 plot combine. Data were processed by analysis of variance (ANOVA). Duncan's multiple range test was used to assess differences between means ($p \leq 0.05$). The least significant difference ($LSD_{0.05}$) was 0.06 t/ha (Dospekhov, 1985). Combining ability was calculated using the method of Sych, Zhemoida, and Sydorka (2004).

RESULTS AND DISCUSSION

The Southern Steppe of Ukraine is characterised by dry summers with high temperatures. The long-term average daily temperature is 19.6°C in June, 22.5°C in July, and 21.0°C in August. However, the soil surface temperature can reach 50°C. Summer precipitation is rare and usually occurs as short showers. Due to high air temperatures, rainfall below 6 mm is scarcely available to plants.

According to long-term data from the Odesa agrometeorological station, the average annual air temperature is 9.6°C, with maximum temperatures reaching 30°C. The sum of temperatures above 10°C reaches 3200–3400 degree-days. Annual precipitation is about 350–390 mm. Mean relative air humidity is 62%, and the hydrothermal coefficient is 0.7–0.8.

During the study years (2020–2023), no substantial fluctuations in air temperature were observed (Figure 1). The highest air temperatures occurred in July and August, followed by a gradual decrease. During the growing season (April–September), average monthly temperatures ranged from 10.3°C to 24.2°C.

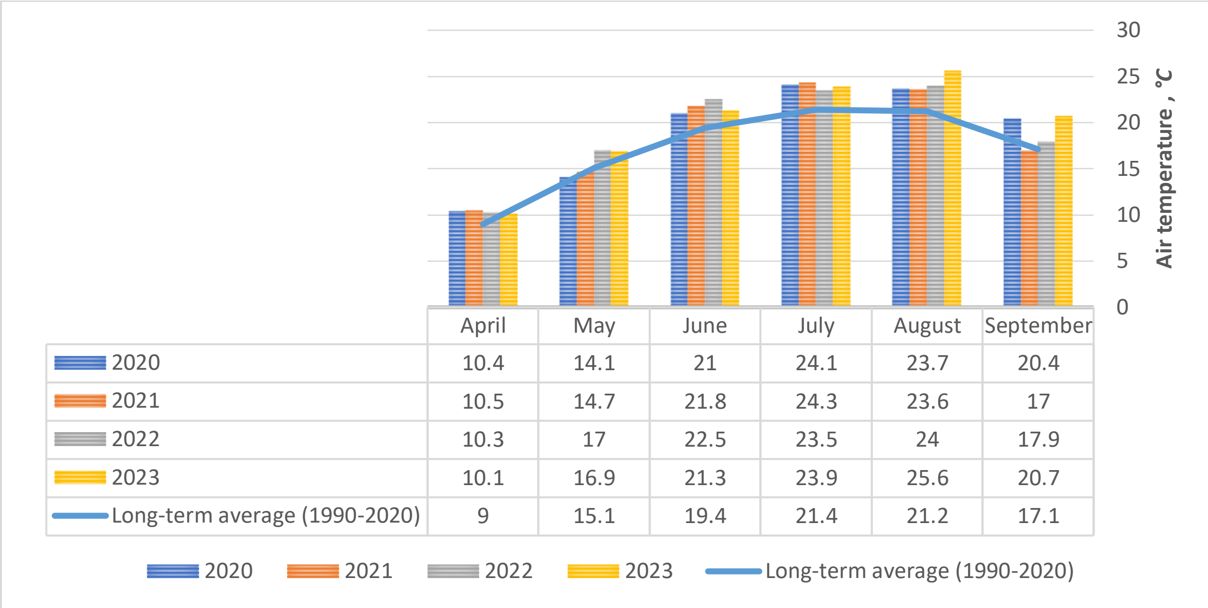

Figure 1. Average monthly air temperature during the growing season (April-September) in 2020-2023, °C

During the four research years, relatively hot summers with insufficient precipitation were observed (Figure 2).

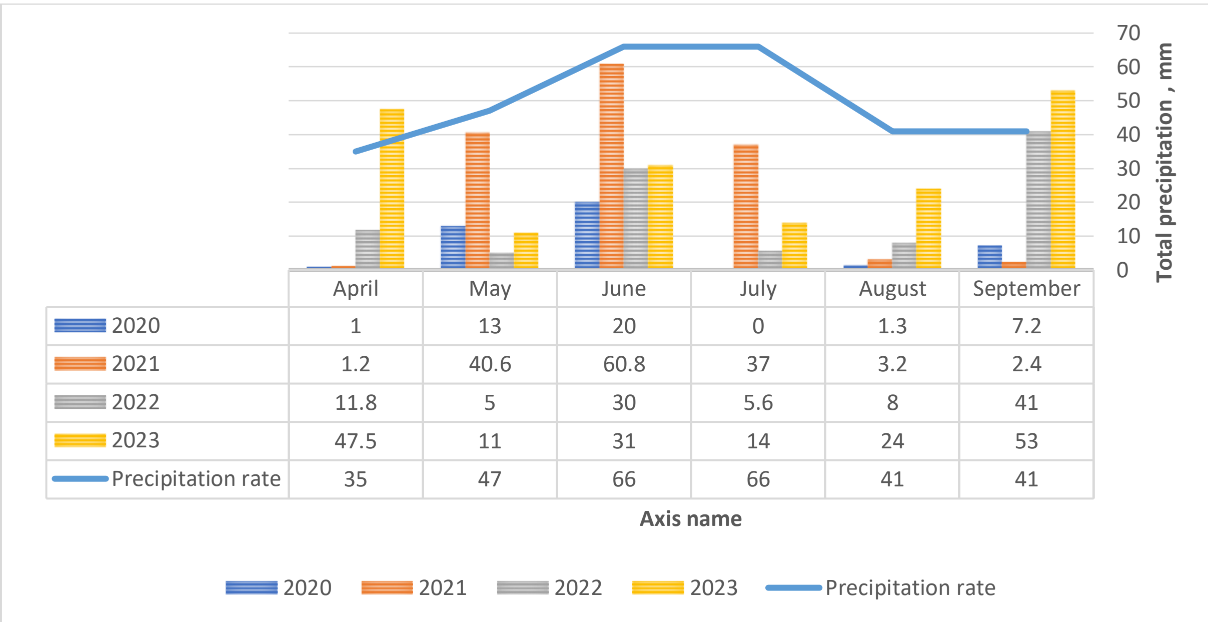

Figure 2. Total precipitation during the growing season (April-September) in 2020-2023, mm

Weather conditions varied among the study years, which was reflected in sunflower hybrid yield (Table 1).

Table 1. Parameters of variation in the yield of sunflower hybrid seeds, t/ha

Parameters		2020	2021	2022	2023
Average ($\bar{x}$) $\pm t_{s(\bar{x})}$		1.23±0.04	1.20±0.12	1.02±0.04	1.55±0.07
V, %		17.29	29.11	20.03	17.11
Lim	min	0.87	0.49	0.59	0.96
	max	1.63	1.86	1.34	2.08
Number of samples (N)		59	58	48	60

Analysis of sunflower hybrid yield in 2020–2023 showed the highest mean yield in 2023 (1.55±0.07 t/ha). The lowest mean yield was recorded in 2022 (1.02±0.04 t/ha), likely due to unfavourable weather conditions and other stress factors. In 2020 and 2021, mean yields were 1.23±0.04 and 1.20±0.12 t/ha, respectively.

The greatest yield variability was observed in 2021 (V = 29.11%), indicating substantial differences among hybrid combinations. The lowest coefficient of variation was recorded in 2023 (17.11%), suggesting a more uniform yield distribution. In 2020 and 2022, variability was 17.29% and 20.03%, respectively.

Minimum yield ranged from 0.49 t/ha in 2021 to 0.96 t/ha in 2023, whereas maximum yield reached 2.08 t/ha in 2023, the highest value for the study period. In 2021, the wide range (0.49–1.86 t/ha) suggests pronounced differences in the genetic potential of hybrids and/or their response to growing conditions. Overall, 2023 combined the highest yield with the greatest stability, while 2021 was characterised by the highest variability.

Over many years of research, 40 inbred sunflower lines resistant to sulfonylurea herbicides have been developed. Marker-assisted selection was actively used in their breeding (Solodenko, Ilchenko, & Varenyk, 2018), which significantly increased the efficiency of the breeding process. The use of molecular markers ensured accurate control of the inheritance of resistance to sulfonylurea herbicides in subsequent generations, which is an important step in developing source material for further breeding.

In this study, tester crosses were used to evaluate a large number of inbred sunflower lines. To improve the accuracy of combining ability estimates, testers with different genetic backgrounds, including genetically distant forms, were used, which, according to Malik (2004), increases the reliability of evaluating general combining ability effects. Using several testers also made it possible to estimate GCA and SCA effects more robustly for the studied lines.

Lines were crossed with testers to produce testcrosses, which were used to estimate "line × tester" interaction effects. This approach enabled characterisation of genetic interactions underlying hybrid yield and supported comparative evaluation of parental components. As noted by Makarchuk (2021), using lines as testers can facilitate rapid identification of forms with high general combining ability and improve the efficiency of selecting promising hybrid combinations.

The results made it possible to differentiate the studied lines according to their GCA and SCA levels and to identify potential directions for their practical use in developing productive sunflower hybrids adapted to unstable moisture conditions in the Southern Steppe of Ukraine.

The detection of relevant specific relationships is significantly influenced by testers; therefore, it is important to select genotypes based on their ability to differentiate regarding the traits that are to be studied (Table 2).

Table 2. Effects of the GCA and variances of the SCA testers on the "seed yield" trait, t/ha

Tester name	Effects GCA g(i)				Variances SCA (σ_{si}^2)			
	2020	2021	2022	2023	2020	2021	2022	2023
Od1002 A	0.16	-0.20	0.07	0.14	0.01	0.13	0.01	0.03
Od1008 A	0.02	0.30	-0.11	-0.20	0.00	0.06	0.03	0.05
Od1042 A	-0.23	-0.09	0.03	0.04	0.01	0.06	0.01	0.03
$LSD_{0,05}$ g(i)	0.10	0.13	0.06	0.07	-	-	-	-

Note: The sum of the effects of the GCA is not equal to 0, since the calculations were carried out in an incomplete testcross system.

The "seed yield" trait is characterized by continuous variability and fluctuates in the range from minimum to maximum. One peculiarity of this trait is the complex nature of its inheritance. It is controlled not by a single gene, but by a large number of genes.

The level of its manifestation substantially depends on the number of dominant genes and the influence of environmental factors. As a result, the variability of the "seed yield" trait consists of genotypic and environmental components.

The effects of the GCA characterise the average contribution of the tester to the productivity of hybrids created with its participation.

The tester Od 1002 A proved positive effects in 2020 (0.16), 2022 (0.07) and 2023 (0.14), which indicates its stable effect on yield. However, in 2021 the effect was negative (-0.20), which may be due to unfavourable growing conditions.

Tester Od 1008 A revealed the best effect in 2021 (0.30), indicating a high positive combining ability in this year. However, in 2022 (-0.11) and 2023 (-0.20), its effects were negative, which may limit its use.

Tester Od 1042 A had a negative effect in 2020 (-0.23) and 2021 (-0.09), indicating its weak potential in these years. In 2022 (0.03) and 2023 (0.04), the effects were slightly positive, indicating an improvement in its impact on yield.

The reliability (LSD 0.05) shows that effects that exceed the threshold values: 0.10 in 2020, 0.13 in 2021, 0.06 in 2022 and 0.07 in 2023 can be considered significant. Accordingly, in 2021, the tester Od 1008 A had a statistically significant positive effect (0.30), and in 2020, Od 1042 A had a significant negative effect (-0.23).

The analysis of variance of the SCA (σsi^2) reflects the interaction level of the tester with other lines, that is, its ability to create effective combinations.

Tester Od 1002 A had the highest variability of the SCA in 2021 (0.13), indicating a strong genotype-environment impact. In other years, the indicators were low (0.01–0.03), indicating stable combination traits.

Tester Od 1008 A had average values of the SCA variance (0.00–0.06), with relatively higher values in 2021 (0.06) and 2023 (0.05). This indicates a change in its combination potential depending on the year.

Tester Od 1042 A had relatively low values of the SCA variance (0.01–0.06), which may indicate a lower ability to create effective combinations or a more stable interaction with other lines.

Tester Od 1002 A is one of the most stable in terms of the GCA indicators, as it demonstrated positive effects in three out of four years. However, in 2021 its effect was negative (-0.20), and the variance of the SCA was the highest (0.13), which may indicate instability in this year.

Tester Od 1008 A had the best GCA effects in 2021 (0.30), albeit in other years its effects were insignificant or negative. The variance of the SCA showed that there was a large variability in its combining ability in 2021 and 2023.

Tester Od 1042 A generally had low GCA effects, especially in 2020 (-0.23) and 2021 (-0.09), indicating its low breeding potential. The low variances of the SCA indicate the relative stability of its combining characteristics.

Tester Od 1002 A is advisable to use for creating stable hybrids, but its variability in certain years must be taken into account. Od 1008 A may be effective in favourable years, but the instability of the GCA effects may limit its use. Od 1042 A has a low breeding potential due to the relatively weak GCA effects.

The assessment of general combining ability showed that among the studied lines, there were forms whose crossing resulted in hybrids with seed yield exceeding standard samples. At the same time, analysis of specific combining ability made it possible to identify individual pairs of lines that formed highly heterotic hybrids with increased productivity.

It was found that the contribution of the SCA dispersion to the total variability of the trait prevailed over the share of the GCA. This indicates the leading role of additive effects in controlling the studied traits and confirms the feasibility of using such lines as donors, which are adapted to unstable moisture conditions for further breeding work. The advantage of additive variation ensured better expression of the genotypic characteristics of the parental components and contributed to more effective selection of forms with high breeding value.

Analysis of the effects of combining ability under different conditions and in different years of cultivation showed significant variability in their expression. It was found that the stability of the expression of GCA and SCA was crucial for the selection of promising parental forms suitable for creating highly productive hybrids. The results obtained showed that some of the lines maintained high breeding value under different environmental conditions, in particular under the unstable moisture conditions of the Southern Steppe of Ukraine, indicating their suitability as stable donors for breeding.

The obtained test crosses were tested in 2020-2023. The overall combining ability of inbred lines was determined by the magnitude of the estimates of the GCA effects. Based on the analysis, all lines were divided into three classes:

1) lines whose GCA effects estimates significantly exceeded the average in the experiment;

2) lines with average GCA indicators;

3) lines whose GCA effects estimates are significantly lower than the average values.

This distribution allows us to objectively assess and classify inbred sunflower lines according to their breeding value, which contributes to a more effective use of the source material in further research.

Analysing the combining ability of inbred sunflower lines according to the characteristic "seed yield", it is worth noting the significant variability of the estimates of the GCA effects depending on the conditions of the year (Figure 3).

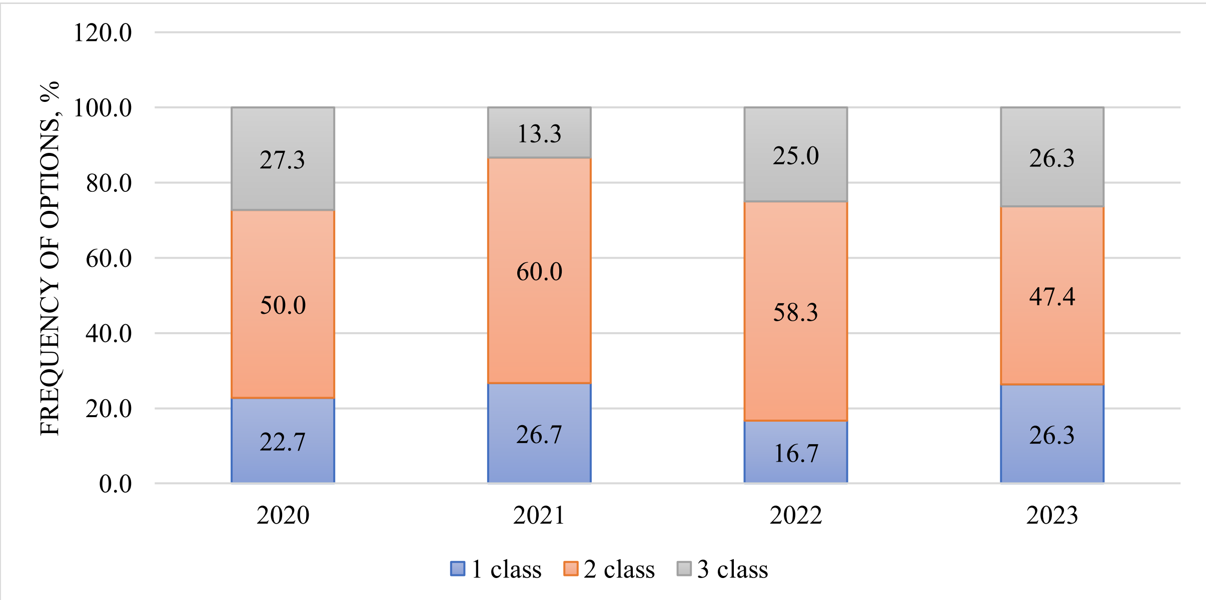

Figure 3. Distribution of sunflower inbred lines into classes in relation to the GCA effects by the "grain yield" trait, %.

Figure 3 shows the distribution of inbred sunflower lines by combining ability classes depending on the GCA effects on seed yield in 2020-2023.

High variability of GCA effects in different years. The share of families with high GCA effects (class 1, blue) varies within 16.7–26.7%, which shows the instability of this indicator in different years. The lowest values were recorded in 2022 (16.7%), and the highest in 2023 (26.3%).

Dominance of the average level of GCA effects (class 2). In all years, class 2 occupies the largest share, which indicates the predominance of average values of combining ability. The largest share of such lines is observed in 2021 (60.0%) and 2022 (58.3%), while in 2023 this figure decreased to 47.4%.

Variability of the part of lines with low GCA effects (class 3) is noticeable. In 2021, the lowest number of inbred lines of this class is noted (13.3%), while in 2020 and 2023 this figure is higher (27.3% and 26.3%, respectively).

In 2021 and 2022, there was a decrease in the proportion of sunflower lines of classes 1 and 3 in favour of class 2, which may indicate less favourable conditions for detecting high or low GCA effects.

In 2023, an increase in the proportion of lines with extreme values (classes 1 and 3) is observed, which may be the result of changes in weather conditions or other influencing factors. The results confirm the significant variability of the effects of the GCA depending on the conditions of the year, indicating the influence of the environment on the realisation of genetic potential. Instability in the distribution of classes can complicate the breeding process and requires the assessment of the GCA effects in multi-year studies.

The study of the combining ability of inbred sunflower lines was carried out during 2020-2023 to assess their GCA and SCA based on the trait "seed yield". Data analysis allows us to identify the most promising lines for further use in breeding programs.

The following table shows the values of the GCA and SCA for the best lines studied, as well as the threshold value of the least significant difference (LSD), which is used to assess the statistical significance of the differences between the results.

The values of the GCA reflect the overall genetic ability of the line to deliver high levels of yield, while the SCA indicates its effectiveness in specific hybrid combinations. High GCA values indicate stable productivity of the line, while high SCA values indicate the possibility of obtaining high-yielding hybrids when combined with other genotypes (Table 3).

Table 3. The best lines by combining ability parameters in relation to seed yield, t/ha

Title	2020		2021		2022		2023	
	GCA	SCA	GCA	SCA	GCA	SCA	GCA	SCA
OSU 1534 R	0.23	0.01	0.28	0.01	0.20	0.01	0.36	0.16
OSU 1539 R	0.12	0.03	0.09	-0.01	0.04	0.00	0.07	0.01
OSU 1546 R	0.16	0.06	0.18	0.24	0.12	0.01	0.18	0.09
OSU 1548 R	0.13	0.02	0.09	0.25	0.07	0.00	0.08	0.00
OSU 1549 R	0.14	-0.01	0.15	0.53	0.09	0.01	0.15	0.03
OSU 1551 R	0.14	0.01	0.14	0.17	0.09	0.00	0.15	0.00
OSU 1552 R	0.18	0.04	0.18	0.04	0.17	0.11	0.18	0.03
$LSD_{0,05}$	0.13	0.06	0.14	0.07	0.12	0.06	0.09	0.04

An analysis of precipitation dynamics in 2020–2023 in the Southern Steppe of Ukraine showed significant fluctuations in rainfall relative to the climatic norm (Figure 2). Conditions in 2020 and 2021 were particularly critical, when, during the period of active growth and seed filling (June–July), precipitation was markedly below the norm (20 mm in June 2020, compared with 66 mm; 37 mm in July 2021, compared with 66 mm). In 2022, there was also a moisture deficit in May and July, whereas 2023 was characterised by relatively favourable conditions, especially in September (53 mm compared with 41 mm).

Insufficient moisture in the conditions of the Southern Steppe of Ukraine significantly affected the manifestation of the combining ability of lines. In conditions of precipitation deficit, lines with high general combining ability had an advantage, which indicates the stability of additive effects and better genetic fixation of productivity traits. Thus, OSU 1534 R demonstrated the highest values of GCA in all years, with a maximum in 2023 (0.36), which confirms its high ecological flexibility and stability of yield inheritance regardless of the level of moisture. Stability of GCA values was also observed in OSU 1552 R (0.17–0.18 in all years) and OSU 1546 R (0.12–0.18), making them suitable for use as reliable donors adapted to conditions of insufficient moisture.

As for specific combining ability, its manifestation proved to be more dependent on weather conditions. Thus, in 2021, when there was a moisture deficit in June-July, high SCA values were recorded in OSU 1549 R (0.53) and OSU 1548 R (0.25). This indicates that their potential is expressed under stress conditions due to non-additive genetic effects and heterotic interactions. In contrast, in the more favourable year of 2023, OSU 1546 R (0.09) and OSU 1534 R (0.16) had increased SCA, indicating the possibility of forming productive combinations with sufficient moisture availability.

Thus, the variability of GCA and SCA manifestations in different years is directly associated with the hydrothermal conditions of the Southern Steppe of Ukraine. The most stable and reliable under different conditions were OSU 1534 R, OSU 1546 R, and OSU 1552 R, which maintained a high level of inherited productivity regardless of weather conditions. However, OSU 1549 R and OSU 1548 R showed high SCA only in the conditions of 2021, this indicates their potential suitability for use in hybrid combinations adapted to dry conditions of the Southern Steppe.

CONCLUSION

The analysis of the combining ability of inbred sunflower lines in 2020–2023 under the conditions of the Southern Steppe of Ukraine allowed their breeding value to be assessed for the trait "seed yield". Significant variability in general and specific combining ability was established depending on hydrothermal conditions and genotype, confirming the feasibility of multi-year trials.

1. The lines OSU 1534 R, OSU 1546 R, and OSU 1552 R demonstrated consistently high values of the GCA throughout the years of the study, which indicates their ecological plasticity, genetic stability, and high tolerance to dry conditions. These lines are promising for use as reliable donors in breeding for yield.
2. The highest SCA values were recorded in hybrid combinations involving OSU 1549 R and OSU 1548 R lines in 2021, demonstrating their ability to realise their productive potential under water stress conditions due to non-additive genetic effects. In the favourable year of 2023, OSU 1546 R and OSU 1534 R had increased SCA, confirming their adaptability to different moisture conditions.
3. It has been established that weather conditions, especially precipitation levels during critical phases of plant development, have a significant impact on the manifestation of combining ability. This highlights the importance of long-term testing of genotypes in different environmental conditions for a reliable assessment of their breeding value.

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