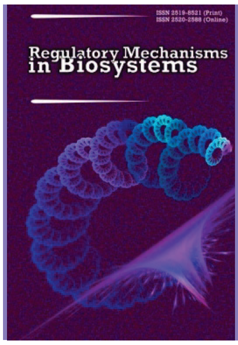

Regulatory Mechanisms
in Biosystems

ISSN 2519-8521 (Print)
ISSN 2520-2588 (Online)
Regul. Mech. Biosyst.,
2022, 13(2), 197–206
doi: 10.15421/022225

Elucidation of gene action and combining ability for productive tillering in spring barley

V. M. Hudzenko*, T. P. Polishchuk*, A. A. Lysenko*, I. V. Fedorenko*, M. V. Fedorenko*, L. V. Khudolii**, V. A. Ishchenko***, H. M. Kozelets***, A. I. Babenko****, S. P. Tanchyk****, S. M. Mandrovska*****

**The V. M. Remeslo Myronivka Institute of Wheat of National Academy of Agrarian Sciences of Ukraine, Tsentralne, Ukraine*
***Institute of Plant Variety Examination, Kyiv, Ukraine*
****Institute of Agriculture of Steppe of National Academy of Agrarian Sciences of Ukraine, Sozonivka village, Ukraine*
*****National University of Life and Environmental Sciences of Ukraine, Kyiv, Ukraine*
******Institute of Bioenergy Crops and Sugar Beet of National Academy of Agrarian Sciences of Ukraine, Kyiv, Ukraine*

Article info

Received 06.04.2022
Received in revised form 03.05.2022
Accepted 04.05.2022

The V. M. Remeslo Myronivka Institute of Wheat of National Academy of Agrarian Sciences of Ukraine, Tsentralna st., 68, Tsentralne village, Kyiv region, 08853, Ukraine. Tel.: +38-096-879-38-00. E-mail: barley22@ukr.net

Institute of Plant Variety Examination, Henerala Rodymtseva st., 15, Kyiv, 03041, Ukraine. Tel.: +38-097-947-77-02. E-mail: hudoliyl4@gmail.com

Institute of Agriculture of Steppe of National Academy of Agrarian Sciences of Ukraine, Tsentralna st., 2, Sozonivka village, Kropyvnytskyi district, Kirovohrad region, 27602, Ukraine. Tel.: +38-096-994-22-45. E-mail: semena2013@ukr.net

National University of Life and Environmental Sciences of Ukraine, Heroiv Oborony st., 12, Kyiv, 03041, Ukraine. Tel.: +38-099-528-96-25. E-mail: babenkoantonina@ukr.net

Institute of Bioenergy Crops and Sugar Beet of National Academy of Agrarian Sciences of Ukraine, Klinichna st., 25, Kyiv, 03080, Ukraine. Tel.: +38-097-953-94-50. E-mail: mandrovskasveta@gmail.com

Hudzenko, V. M., Polishchuk, T. P., Lysenko, A. A., Fedorenko, I. V., Fedorenko, M. V., Khudolii, L. V., Ishchenko, V. A., Kozelets, H. M., Babenko, A. I., Tanchyk, S. P., & Mandrovska, S. M. (2022). Elucidation of gene action and combining ability for productive tillering in spring barley. Regulatory Mechanisms in Biosystems, 13(2), 197–206. doi:10.15421/022225

The purpose of the present study is to identify breeding and genetic peculiarities for productive tillering in spring barley genotypes of different origin, purposes of usage and botanical affiliation, as well as to identify effective genetic sources to further improving of the trait. There were created two complete (6 × 6) diallel crossing schemes. Into the Scheme I elite Ukrainian (MIP Tytul and Avhur) and Western European (Datcha, Quench, Gladys, and Beatrix) malting spring barley varieties were involved. Scheme II included awnless covered barley varieties Kozyr and Vitrazh bred at the Plant Production Institute named after V. Y. Yuriev of NAAS of Ukraine, naked barley varieties Condor and CDC Rattan from Canada, as well as awned feed barley variety MIP Myroslav created at MIW and malting barley variety Sebastian from Denmark. For more reliable and informative characterization of barley varieties and their progeny for productive tillering in terms of inheritance, parameters of genetic variation and general combining ability (GCA) statistical analyses of experimental data from different (2019 and 2020) growing seasons were conducted. Accordingly to the indicator of phenotypic dominance all possible modes of inheritance were detected, except for negative dominance in the Scheme I in 2020. The degree of phenotypic dominance significantly varied depending on both varieties involved in crossing schemes and conditions of the years of trials. There was overdominance in loci in both schemes in both years. The other parameters of genetic variation showed significant differences in gene action for productive tillering between crossing Schemes. In Scheme I in both years the dominance was mainly unidirectional and due to dominant effects. In the Scheme II in both years there was multidirectional dominance. In Scheme I compliance with the additive-dominant system was revealed in 2019, but in 2020 there was a strong epistasis. In Scheme II in both years non-allelic interaction was identified. In general, the mode of gene action showed a very complex gene action for productive tillering in barley and a significant role of non-genetic factors in phenotypic manifestation of the trait. Despite this, the level of heritability in the narrow sense in both Schemes pointed to the possibility of the successful selection of individuals with genetically determined increased productive tillering in the splitting generations. In Scheme I the final selection for productive tillering will be more effective in later generations, when dominant alleles become homozygous. In Scheme II it is theoretically possible to select plants with high productive tillering on both recessive and dominant basis. In both schemes the non-allelic interaction should be taken into consideration. Spring barley varieties Beatrix, Datcha, MIP Myroslav and Kozyr can be used as effective genetic sources for involvement in crossings aimed at improving the productive tillering. The results of present study contribute to further development of studies devoted to evaluation of gene action for yield-related traits in spring barley, as well as identification of new genetic sources for plant improvement.

Keywords: *Hordeum vulgare* L.; phenotypic dominance; mode of inheritance; parameters of genetic variation; general combining ability.

Introduction

Barley (*Hordeum vulgare* L.) is one of the most economically important crops in world-wide agriculture. Barley is used for very various purposes. The most predominant trends of usage are feed for different types of animals, malting and food industries. In accordance with the above-mentioned, there are three main directions of barley breeding in terms of quality. Each of the trends has certain requirements for the grain properties, which for the malting barley are opposed to feed and food purposes of use (Fang et al., 2019; Guo et al., 2020; Rani et al., 2021). The most suitable for malting are "traditional" covered awned barley varieties (Laidig et al., 2017; Gamayunova et al., 2021; Habschied et al., 2021; Ishchenko & Kozelets, 2021). Great advances in malting barley breeding have been achieved in Western Europe, as well as in some other countries of the World (Edney et al., 2014; Matthies et al., 2014; Mastanjević et al., 2017). Naked barley has a great potential as functional food for humans and high-quality feed for animals (Yang et al., 2018; Habiyaremye et al., 2021). It is characterized by high protein content and many other important nutrients

(Shaveta et al., 2019). For example, barley flour is used to improve (fortify) the quality of products made from wheat flour (Narwal et al., 2017; Sterna et al., 2021). Thorough genetic and breeding studies of naked barley are conducted in Canada and some Asian countries (Yuan et al., 2012; Yao et al., 2018; Yadav et al., 2018). Awnless barley varieties have practical value for dual-purpose usage (forage grain and straw) in animal feeding (Kompanets & Kozachenko, 2017). Breeding programs for different purposes of barley usage are carried out in different countries (Naumov et al., 2014; Assefa et al., 2021). In spite of the above mentioned trends of usage and botanical affiliation commercial barley varieties must combine a high grain yield with a set of other agronomic and adaptive traits and capacities (Kassie et al., 2018; Tokhetova et al., 2020; Bohačenko et al., 2021).

Barley grain yield is a result of the productivity of individual plants and their number per unit area. In turn, the productivity of a barley plant is a complex trait. It is a result of the productive tiller number per plant, kernel number per spike and kernel weight. Thus, one of the main structural elements of grain productivity of barley plant is productive tillering. A tiller is a shoot which forms at ground level in the angle between a leaf and the main shoot in a barley plant, as well as some other crops, such as wheat, oats, rye, etc. Productive tillers with fertile spikes (true stems) are only produced from the tillers at a later stage of the plant development. Some tillers remain non-productive and have no spikes. Information about genetic mechanisms controlling tiller development is important for designning optimal shoot features to maximize barley plant productivity (Dockter et al., 2014; Abdel-Ghani et al., 2019; Shaaf et al., 2019). Based on numerous genetic studies of barley mutants, the following genes have been identified and marked as associated with no tillering – gene *cul2* on the chromosome *6HL* (Babb & Muehlbauer, 2003; Druka et al., 2011; Okagaki et al., 2013), low tillering – *als1*, *cul4*, *lnt1* on the chromosome *3HL*, *int-b* on *5HL*, *ops1* on *7HS* (Dabbert et al., 2009; Dabbert et al., 2010; Tavakol et al., 2015) and as associated with increased tillering – grassy (Hussien et al., 2014), *mnd1* on *2H*, *mnd5* on *7HL*, *mnd3* on *4HS*, and *mnd6* on *5HL* (Franckowiak & Lundqvist, 2013), *HvD14* on *4H* (Marzec et al., 2016), *sdw1* on *3HL* (Xu et al., 2017).

The final tillerring is determined by the developmental process of the plant, soils and atmospheric stimuli, and is regulated by a complex network of hormonal activity (Bauer & Wirén, 2020; Koprna et al., 2021). It was established that *HvHNT1* which encodes a trypsin family protein controls tiller development through *HvPPIase* (Ye et al., 2019). Lower expression levels of *HvD27*, *HvMAX1*, *HvCCD7*, and *HvCCD8* genes indicated that abscisic acid suppresses strigolactones hormones biosynthesis, that are involved in inhibiting shoot branching and in promoting abiotic stress responses, and lead to enhanced tiller formation in barley (Wang et al., 2018). The marker-based studies of barley have identified numerous quantitative trait loci (QTLs) associated with tillering (Haaning et al., 2020; Li et al., 2020; Riaz et al., 2021), as well as in several other main crops, such as wheat (Wang et al., 2016; Liu et al., 2018), rice (He et al., 2017) and sorghum (Kong et al., 2014). The interrelated effects of genes associated with tillering and genes that control other morphological traits of the barley plant have been identified (Nadolska-Orczyk et al., 2017). Highly significant links were revealed between the genetic control of tillering and row-type (Jia et al., 2011; Ramsay et al., 2011; Liller et al., 2015), as well as the influence of genes associated with photoperiodic and vernalization sensitivity, circadian rhythms, etc. (Naz et al., 2014; Alqudah et al., 2016; Nice et al., 2017). In a recent study (Bai et al., 2021), single-nucleotide polymorphisms' loci associated with tillering in hulless barley have been identified using the genome-wide specific length amplified fragment sequencing method via high throughput sequencing technology. Moreover, results showed that tillering was affected by the combination of genetic and non-genetic factors.

The purpose of the present study is to identify breeding and genetic peculiarities for productive tillering in spring barley genotypes of different origin, purposes of usage and botanical affiliation, as well as to identify effective genetic sources to further improvement of the trait.

Materials and methods

The peculiarities of gene action for productive tillering in F_1 of spring barley were studied in two complete (6 × 6) diallel crossing schemes at the V. M. Remeslo Myronivka Institute of Wheat of NAAS of Ukraine (MIW). Into the Scheme I we involved elite Ukrainian (MIP Tytul and Avhur) and Western European (Datcha, Quench, Gladys, and Beatrix) malting spring barley varieties. Into the Scheme II we involved awnless covered barley varieties Kozyr and Vitrazh bred at the Plant Production Institute named after V. Y. Yuriev of NAAS of Ukraine, naked barley varieties Condor and CDC Rattan from Canada, as well as awned feed barley variety MIP Myroslav created at MIW and malting barley variety Sebastian from Denmark. Thus, the studied varieties are different in the purpose of usage, geographical origin and botanical affiliation. Plants of the parent components and F_1 were grown in field conditions in three randomized replications (rows). Distance between plants in row was 5 cm, and between rows was 15 cm. Analysis of yield components of the bundle material (no less than 25 plants) was performed from each replication.

MIW is located in the central part of the Forest-Steppe of Ukraine (49°64′ N, 31°08′ E, altitude is 153 m). Soils are deep, little humus, slightly leached chornozem. Humus content 3.8%, alkaline hydrolysed nitrogen – 59.0 mg/kg, P_2O_5 – 220.1 mg/kg, K_2O – 96.0 mg/kg, pH = 5.8. For more reliable and informative characterization of barley varieties and their progeny we conducted statistical analyses of experimental data from 2019 and 2020 growing seasons. The main difference between two growing seasons in weather conditions consisted in the significantly lower average monthly air temperature in May 2020 (+12.8 °C) as compared to 2019 (+17.3 °C). In this term May 2020 was also significantly different from an average long-term value (+16.2 °C). Along with that, the monthly amount of precipitation (91.6 mm) in May 2020 significantly exceeded the value of 2019 (50.9 mm), as well as average long-term amount (56.4 mm). The average monthly temperature in June exceeded the average long-term value (+19.5 °C) both in 2019 (+22.6 °C) and in 2020 (+21.7 °C). It should be noted that the amount of precipitation in June, on the contrary, in 2019 (86.8 mm) was close to average long-term values (82.7 mm), and in 2020 it was significantly lower (57.1 mm).

The degree of phenotypic dominance in F_1 was calculated according to a well-known method (Beil & Atkins, 1965). The combination ability and parameters of genetic variation were determined according to the original works (Hayman, 1954, 1958, 1960) and (Griffing, 1956a, 1956b). Computer program Statistica 12 were used for calculations. Tables 1, 2 and Figure 3 demonstrate the results as x ± SE (mean ± standard error). Differences among the values of the experimental variants were calculated using ANOVA with Bonferroni correction, where the differences were considered significant at $P < 0.05$.

Results

Manifestation level and phenotypic dominance. Table 1 shows the manifestation level of productive tillering in parental components and their hybrids in the Scheme I. The manifestation level of productive tillering in 2019 among parental components varied from 4.79 ± 0.10 tillers in the variety Gladys to 7.17 ± 0.06 tillers in the variety Datcha. The maximum value of the trait was in the hybrid combination Beatrix / MIP Tytul (7.73 ± 0.15 tillers), the minimum value was in the combination MIP Tytul / Gladys (5.20 ± 0.10 tillers). In 2020, the grand mean (average on the whole experiment) level of productive tillering was higher (7.79 tillers), as compared to 2019 (6.25 tillers). The highest productive tillering performance in parental components (8.10 ± 0.17 tillers) was in the variety Quench, and the poorest performance (6.93 ± 0.12 tillers), as in the previous year, was in the variety Gladys. The highest manifestation level was in the hybrid combination Beatrix / MIP Tytul (9.07 ± 0.12 tillers), and the lowest level was in the hybrid combination MIP Tytul / Gladys (7.10 ± 0.05 tillers). It should also be noted that the variety Gladys had the greatest difference in the trait manifestation level between two years (2.14 tillers). Among F_1, the greatest difference between years was observed in hybrid combination Avhur / Datcha (2.90 tillers). In the variety Datcha the difference of manifestation levels of trait between years was minimal (0.53 tillers). Among F_1 the smallest productive tillering variation was in the combination MIP Tytul / Quench (0.23 tillers). On average for two years the highest manifestation level of the trait was in the varieties Avhur (7.47 ± 0.04 tillers) and Datcha (7.43 ± 0.13 tillers), and the lowest one was in the variety Gladys (5.86 ± 0.11). Thus, variety Datcha combined a high manifestation level of the trait with its relative phenotypic stability in different years. In F_1 the maximal productive tillering was in the hybrid combination Beatrix / MIP Tytul (8.40 ± 0.13 tillers). In accordance with the indicator of phenotypic dominance in 2019 all possible mode of inheritance were found, and also in 2020 except for negative dominance. Along with that, the number of combinations with particular mode of inheritance was different in different years. The positive overdominance was revealed in 2019 in seven combinations and in 2020 in 15 combinations. Positive dominance was noticed in three hybrid combination in both years. Intermediate inheritance in 2009 was in 13 combinations and in 2020 was in eight combinations. Negative dominance was found only in three combinations. In several combinations the mode of inheritance changed in different years. In particular, in three combinations (MIP Tytul / Quench, Datcha / Avhur, and Avhur / Datcha) it varied from positive overdominance to negative overdominance.

In the Scheme II in 2019, manifestation level of the productive tillering in parental components varied from 5.17 ± 0.31 tillers in the variety Kozyr to 4.00 ± 0.05 tillers in the variety CDC Rattan (Table. 2). The maximal value of the productive tillering (6.83 ± 0.40 tillers) was in the hybrid combination MIP Myroslav / Sebastian, and the minimal value (3.71 ± 0.19 tillers) of the trait was in the hybrid combination CDC Rattan / Condor. In 2020, the highest performance among parental components was also in the variety Kozyr (9.33 ± 0.15 tillers), and the poorest performance was in the variety CDC Rattan (6.45 ± 0.18 tillers).

Table 1

Manifestation level and degree of phenotypic dominance for productive tillering in F1 of spring barley (Scheme I) (n = 3 x 25, x ± SE)

Variety (parental component), crossing combination	2019			2020		
	productive tillering, tillers / plant	indicator of phenotypic dominance		productive tillering, tillers / plant	indicator of phenotypic dominance	
		degree	mode		degree	mode
MIP Tytul	5.87 ± 0.12	–	–	7.03 ± 0.06	–	–
MIP Tytul / Beatrix	7.00 ± 0.20	13.13	PO	8.35 ± 0.35	3.89	PO
MIP Tytul / Datcha	6.57 ± 0.21	0.08	II	7.97 ± 0.08	180.00	PO
MIP Tytul / Quench	6.70 ± 0.20	2.30	PO	6.93 ± 0.15	–1.19	NO
MIP Tytul / Gladys	5.20 ± 0.10	–0.24	II	7.10 ± 0.05	2.50	PO
MIP Tytul / Avhur	6.60 ± 0.10	0.42	II	7.52 ± 0.13	5.00	PO
Beatrix	6.03 ± 0.06	–	–	7.57 ± 0.25	–	–
Beatrix / MIP Tytul	7.73 ± 0.15	22.29	PO	9.07 ± 0.12	6.54	PO
Beatrix / Datcha	6.80 ± 0.20	0.35	II	8.83 ± 0.29	18.00	PO
Beatrix / Quench	7.00 ± 0.20	4.71	PO	7.88 ± 0.16	0.19	II
Beatrix / Gladys	6.05 ± 0.13	1.03	PO	7.67 ± 0.21	1.30	PO
Beatrix / Avhur	6.73 ± 0.62	0.62	PD	8.02 ± 0.10	0.94	PD
Datcha	7.17 ± 0.06	–	–	7.70 ± 0.20	–	–
Datcha / MIP Tytul	7.20 ± 0.22	1.05	PO	7.92 ± 0.16	1.65	PO
Datcha / Beatrix	6.62 ± 0.16	0.03	II	8.45 ± 0.25	12.20	PO
Datcha / Quench	6.70 ± 0.17	–0.17	II	8.40 ± 0.36	2.50	PO
Datcha / Gladys	6.10 ± 0.20	0.10	II	7.75 ± 0.30	1.13	PO
Datcha / Avhur	6.27 ± 0.15	–5.53	NO	8.55 ± 0.13	4.18	PO
Quench	6.37 ± 0.15	–	–	8.10 ± 0.17	–	–
Quench / MIP Tytul	5.92 ± 0.10	–0.79	ND	7.43 ± 0.21	–0.25	II
Quench / Beatrix	6.48 ± 0.03	1.67	PO	8.00 ± 0.10	0.63	PD
Quench / Datcha	6.17 ± 0.14	–1.49	NO	7.88 ± 0.08	–0.08	II
Quench / Gladys	5.70 ± 0.13	0.15	II	7.72 ± 0.10	0.34	II
Quench / Avhur	6.80 ± 0.10	0.63	PD	7.72 ± 0.08	–10.50	NO
Gladys	4.79 ± 0.10	–	–	6.93 ± 0.12	–	–
Gladys / MIP Tytul	5.23 ± 0.08	–0.18	II	7.12 ± 0.10	2.86	PO
Gladys / Beatrix	5.48 ± 0.23	0.11	II	7.95 ± 0.35	2.19	PO
Gladys / Datcha	6.47 ± 0.06	0.41	II	7.62 ± 0.20	0.78	PD
Gladys / Quench	5.77 ± 0.21	0.24	II	7.75 ± 0.15	0.40	II
Gladys / Avhur	5.30 ± 0.20	–0.52	ND	7.43 ± 0.52	–0.11	II
Avhur	6.90 ± 0.01	–	–	8.03 ± 0.06	–	–
Avhur / MIP Tytul	6.80 ± 0.20	0.81	PD	7.67 ± 0.15	0.27	II
Avhur / Beatrix	5.83 ± 0.21	–1.45	NO	7.40 ± 0.36	–1.74	NO
Avhur / Datcha	5.33 ± 0.24	–12.28	NO	8.23 ± 0.12	2.24	PO
Avhur / Quench	5.53 ± 0.06	–4.09	NO	7.27 ± 0.21	–24.00	NO
Avhur / Gladys	5.73 ± 0.25	–0.11	II	7.37 ± 0.40	–0.21	II

Note: NO – is for negative overdominance, ND – is for negative dominance, II – is for intermediate inheritance, PD – is for positive dominance, PO – is for positive overdominanc.

The maximal manifestation level of the trait on average for two years was in the variety Kozyr (7.25 ± 0.23 tillers), and the minimal productive tillering was revealed in the variety CDC Rattan (5.23 ± 0.12 tillers). Among F_1 the maximal productive tillering on average for two years was in the hybrid combination Kozyr / MIP Myroslav (8.78 ± 0.23 tillers), and the minimal productive tillering was in the combination CDC Rattan / Kozyr (5.66 ± 0.22 tillers). We should emphasize that in the Scheme II variability in the manifestation level of the productive tillering between years was higher in comparison to the Scheme I. On average for parental components and F_1 in the Scheme II it was 3.42 tillers. At the same time, in the Scheme I it was 1.54 tillers. The greatest difference in manifestation level of the productive tillering between two years was in the variety Kozyr (4.17 tillers), and the least difference was in the variety Sebastian (2.17 tillers). Thus, despite the variety Kozyr having the highest manifestation level of the trait it was the most variable depending on conditions of the years. Among F_1 the maximal difference in the manifestation level was in the hybrid combination Kozyr / Vitrazh (5.50 tillers), and the minimal difference was in the combination MIP Myroslav / Sebastian (1.40 tillers). In 2019 positive overdominance was detected in 14 combinations, and in 2020 it was in 17 combinations. Three combinations had positive dominance in both years. Intermediate inheritance in 2019 was revealed in five combinations, and in 2020 it was found in seven combinations. Negative dominance was in one combination in each year. As in the Scheme I, we established changes in mode of inheritance in several combinations. The most radical shift from positive overdominance to negative overdominance was revealed in six combinations Kozyr / Vitrazh, Kozyr / MIP Myroslav, Vitrazh / Kozyr, Vitrazh / MIP Myroslav, MIP Myroslav / Vitrazh, CDC Rattan / Condor.

Parameters of genetic variation. In accordance with the parameters of genetic variation, we found that in both Schemes in both years the effects of dominance prevailed over the additive ones (Table 3). Therefore, in all variants of the experiment, the indicator of average degree of dominance in loci pointed towards overdominance. The parameters of the relative frequency of distribution and the ratio of the total quantity of dominant and recessive alleles indicated the prevalence of dominant effects over recessive in the Scheme I in two years, and in the Scheme II only in 2020. For all variants of the experiment, a strong asymmetry in the distribution of dominant and recessive effects was found.

Table 2
Manifestation level and degree of phenotypic dominance for productive tillering in F_1 of spring barley (Scheme II) (n = 3 x 25, x ± SE)

Variety (parental component), crossing combination	2019			2020		
	productive tillering, tillers / plant	indicator of phenotypic dominance		productive tillering, tillers / plant	indicator of phenotypic dominance	
		degree	mode		degree	mode
Kozyr	5.17 ± 0.31	–	–	9.33 ± 0.15	–	–
Kozyr / Condor	5.53 ± 0.12	2.11	PO	10.63 ± 0.76	2.16	PO
Kozyr / Vitrazh	4.67 ± 0.06	–3.87	NO	10.17 ± 0.29	4.39	PO
Kozyr / Sebastian	5.73 ± 0.31	9.05	PO	8.25 ± 0.30	–0.02	II
Kozyr / MIP Myroslav	6.60 ± 0.40	14.84	NO	10.97 ± 0.06	4.81	PO
Kozyr / CDC Rattan	4.65 ± 0.18	0.11	II	8.60 ± 0.20	0.49	II
Condor	4.52 ± 0.13	–	–	7.08 ± 0.16	–	–
Condor / Kozyr	5.50 ± 0.10	2.01	PO	10.60 ± 0.36	2.13	PO
Condor / Vitrazh	5.32 ± 0.03	2.52	PO	9.02 ± 0.10	1.21	PO
Condor / Sebastian	5.02 ± 0.08	0.95	PD	8.47 ± 0.35	22.71	PO
Condor / MIP Myroslav	6.73 ± 0.21	8.72	PO	8.83 ± 0.32	1.52	PO
Condor / Rattan	4.17 ± 0.07	–0.32	II	9.37 ± 0.32	8.30	PO
Vitrazh	4.97 ± 0.15	–	–	8.83 ± 0.12	–	–
Vitrazh / Kozyr	4.68 ± 0.26	–3.71	NO	9.60 ± 0.10	2.09	PO
Vitrazh / Condor	4.10 ± 0.10	–2.81	NO	8.07 ± 0.15	0.12	II
Vitrazh / Sebastian	4.90 ± 0.17	–3.33	NO	7.38 ± 0.41	–0.78	ND
Vitrazh / MIP Myroslav	5.27 ± 0.23	90.00	PO	8.13 ± 0.12	–2.87	NO
Vitrazh / CDC Rattan	4.48 ± 0.33	0.00	II	7.23 ± 0.15	–0.34	II
Sebastian	5.03 ± 0.15	–	–	7.20 ± 0.17	–	–
Sebastian / Kozyr	5.55 ± 0.05	6.43	PO	8.30 ± 0.26	0.03	II
Sebastian / Condor	4.90 ± 0.13	0.49	II	7.50 ± 0.10	6.14	PO
Sebastian / Vitrazh	5.10 ± 0.10	3.33	PO	8.56 ± 0.29	0.67	PD
Sebastian / MIP Myroslav	6.08 ± 0.23	35.89	PO	8.70 ± 0.20	1.36	PO
Sebastian / CDC Rattan	5.02 ± 0.08	0.97	PD	7.63 ± 0.15	2.16	PO
MIP Myroslav	4.97 ± 0.15	–	–	8.47 ± 0.21	–	–
MIP Myroslav / Kozyr	6.13 ± 0.21	10.32	PO	9.73 ± 0.23	1.94	PO
MIP Myroslav / Condor	5.98 ± 0.23	5.44	PO	9.02 ± 0.10	1.79	PO
MIP Myroslav / Vitrazh	5.50 ± 0.20	160.00	PO	8.08 ± 0.03	–3.15	NO
MIP Myroslav / Sebastian	6.83 ± 0.40	61.11	PO	8.23 ± 0.32	0.63	PD
MIP Myroslav / CDC Rattan	6.10 ± 0.36	3.32	PO	8.20 ± 0.20	0.73	PD
CDC Rattan	4.00 ± 0.05	–	–	6.45 ± 0.18	–	–
CDC Rattan / Kozyr	3.77 ± 0.20	–1.39	NO	7.55 ± 0.25	–0.24	II
CDC Rattan / Condor	3.71 ± 0.19	–2.10	NO	9.18 ± 0.06	7.71	PO
CDC Rattan / Vitrazh	4.00 ± 0.26	–0.99	ND	8.01 ± 0.48	0.31	II
CDC Rattan / Sebastian	4.93 ± 0.15	0.81	PD	7.74 ± 0.25	2.43	PO
CDC Rattan / MIP Myroslav	4.62 ± 0.10	0.27	II	8.20 ± 0.20	445.00	PO

Note: NO – is for negative overdominance, ND – is for negative dominance, II – is for intermediate inheritance, PD – is for positive dominance, PO – is for positive overdominance.

In both crossing schemes in both years the F_1-P index had a positive value, and therefore it showed that the average level of value in hybrids was higher than in the parent components. That is, the dominance was aimed at increasing the trait. In Scheme I, the negative values of the coefficient of correlation of the sum of covariance and variance and the mean value of the trait indicated that in both years the dominance was mainly unidirectional and due to dominant effects. Along with that, in Scheme II in both years the values of the indicator of direction of dominance were not reliable and it pointed towards multidirectional dominance. That is, in Scheme II there are presented recessive effects that lower manifestation of the trait and recessive effects that increase manifestation of the trait, as well as dominant effects that increase manifestation of the trait and dominant effects that lower manifestation of the trait. The coefficient of heritability in the broad sense (H_{bs}) was $H_{bs} = 0.94$ in both years in Scheme II and in 2019 in Scheme I. In 2020 in Scheme I it was $H_{bs} = 0.84$. In general, the coefficient of heritability in the narrow sense (h_{ns}) had significantly lower values in all variants of the experiment. In Scheme I it varied from $h_{ns} = 0.41$ in 2020 to $h_{ns} = 0.58$ in 2019. In Scheme II in 2019 it was $h_{ns} = 0.65$ and in 2020 it was $h_{ns} = 0.54$.

Graphical analysis of the regression of covariance (Wr) on the variance (Vr) confirmed and complemented the information received from parameters of genetic variation. The regression coefficient in Scheme I in 2019 was b = 0.70 ± 0.29, and in 2020 it was b = –0.05 ± 0.31 (Fig. 1). Therefore, we can note that for this set of varieties the productive tillering in 2019 was determined mainly by the additive-dominant system, but in 2020 there was detected a strong non-allelic interaction (epistasis). The epistasis is clearly noticeable on the graphs because of the slope of the regression line. In Scheme II, the value of regression coefficient in 2019 was b = 0.28 ± 0.11, and in 2020 it was b = 0.25 ± 0.15 (Fig. 2). That is, in Scheme II in both years the epistasis was identified.

Table 3
Parameters of genetic variation
for productive tillering in F_1 of spring barley

Parameters of genetic variation	Scheme I		Scheme II	
	2019	2020	2019	2020
D	0.69	0.21	0.17	1.25
H_1	0.94	0.74	1.27	2.49
H_2	0.66	0.54	0.80	1.93
F	0.46	0.16	–0.24	0.49
$\sqrt{H_1/D}$	1.17	1.86	2.72	1.41
$(\sqrt{4DH_1} + F)/(\sqrt{4DH_1} - F)$	1.78	1.51	0.60	1.32
$H_2/4H_1$	0.18	0.18	0.16	0.19
r[(Wr+Vr)I; xi]	–0.52 ± 0.43	–0.66 ± 0.37	–0.06 ± 0.50	0.19 ± 0.49
F_1-P	0.07	0.27	0.41	0.77
H_{bs}	0.94	0.84	0.94	0.94
h_{ns}	0.58	0.41	0.65	0.54

Note: D – is for additive effects, H_1 and H_2 – are for effects of dominance, F – is for the indicator of relative distribution frequency of dominant and recessive alleles, $\sqrt{H_1/D}$ – is for the average degree of dominance in loci $(\sqrt{4DH_1} + F)/(\sqrt{4DH_1} - F)$ – is for the ratio of the total quantity of dominant and recessive alleles, $H_2/4H_1$ – is for average measure of alleles in loci, r[(Wr+Vr)$_i$; x$_i$] – is for the indicator of direction of dominance, F_1-P – is for the indicator of mode of dominance, H_{bs} – is for heritability in broad sense, h_{ns} – is for heritability in narrow sense.

Characteristic of genotypes involved in both diallel crossing schemes by the effects of general combining ability (GCA) are given in Figure 3. In Scheme I significantly high (reliable prevailed over zero point) effects of GCA in both years were found only in two varieties Beatrix (g = 0.39–0.41) and Datcha (g = 0.20–0.41). In the variety MIP Tytul effects of GCA varied from high (g = 0.29) in 2019 to low (g = –0.16) in 2020.

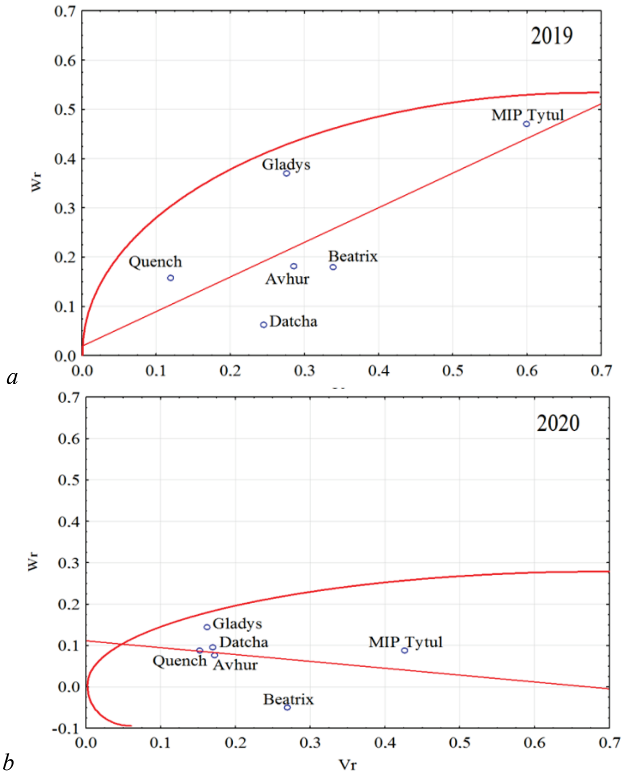

Fig. 1. Graphs of regression Wr / Vr for productive tillering in F_1 of spring barley in the Scheme I: *a* – 2019, *b* – 2020, Vr – variance, Wr – covariance

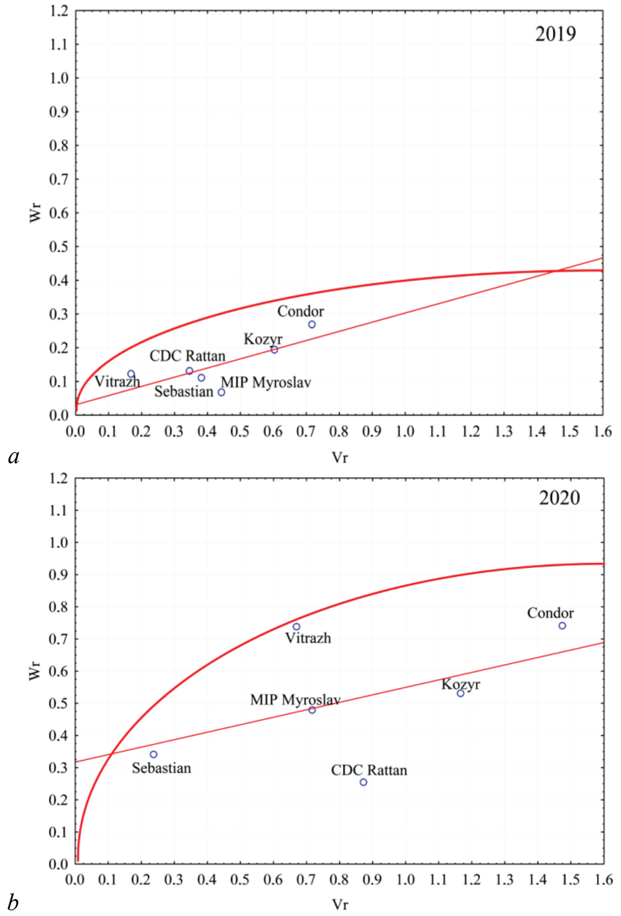

Fig. 2. Graphs of regression Wr / Vr for productive tillering in F_1 of spring barley in the Scheme II: *a* – 2019, *b* – 2020, Vr – variance, Wr – covariance

In the variety Quench effects of GCA were intermediate (do not significantly differ from zero point) in 2019 (g_i = 0.02), and in 2020 they were statistically low (g = –0.17). In both years low effects of GCA were found in the varieties Gladys (g = –0.70…–0.36) and Avhur (g = –0.21…–0.14). In Scheme II in the variety Kozyr effects of GCA varied from not reliable in 2019 (g_i = 0.12) to highly reliable in 2020 (g = 0.97). In contrast, in the variety MIP Myroslav, effects of GCA were high (g = 1.00) in 2019 and close to margins of reliability in 2020 (g = 0.18). Effects of GCA varied from high to low in varieties Condor (g = –0.11–0.50) and Sebastian (g = –0.74–0.28). Statistically low effects of GCA in both years were found in the varieties Vitrazh (g = –0.48…–0.30) and CDC Rattan (g = –0.80…–0.62).

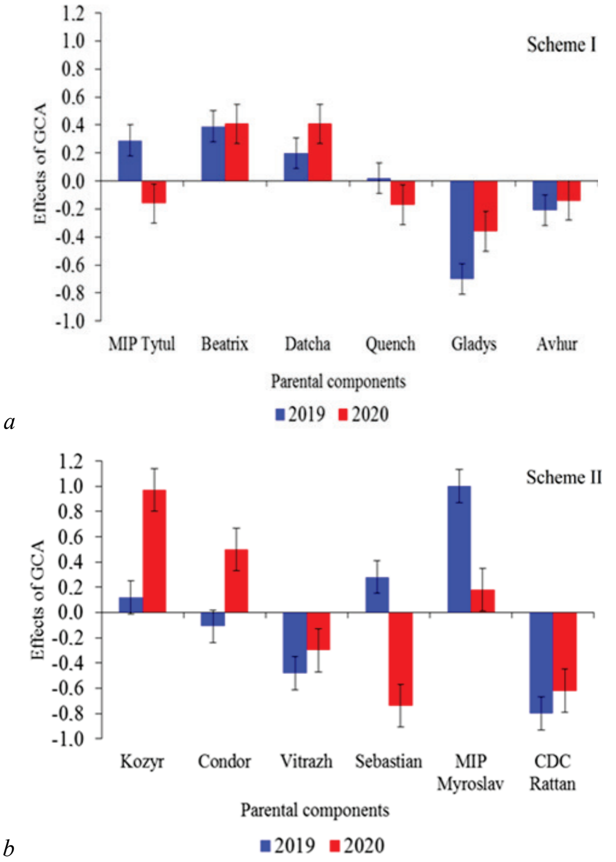

Fig. 3. Effects of general combining ability (GCA) for productive tillering in F_1 of spring barley: *a* – Scheme I, *b* – Scheme II (n = 3 x 25, x ± SE)

Discussion

There were publications in recent years which reported about development of new molecular and genetic methods for genomic selection and genomic hybrid prediction in crops (Philipp et al., 2016; Li et al., 2016; Thorwarth et al., 2017). Such approaches in perspective will be able to significantly increase effectiveness and precision in genetic and breeding experiments (Cui et al., 2020; Wang et al., 2020; Labroo et al., 2021). However, there are several disadvantages of genomic data: they are often difficult to obtain and they still remain too expensive for routine using in plant breeding (Rincent et al., 2018). There are some studies which declared that gemomic approaches are less sufficient for comprehensive prediction phenomic manifestation of traits because of genotype by environment interaction (Govindaraju, 2019). That is why these approaches need to be improved before being widely used in the breeding process (Ansarifar et al., 2020; Jarquin et al., 2021; Widener et al., 2021). Another method, such as phenomic prediction can be also applied at different stages in the breeding process (Fonseca et al., 2021). Presumably, it can successfully compete with genomic selection for predicting complex traits to increase genetic gain in plant breeding (Zhu et al., 2021). Despite the rapid development of genomic and phenomic technologies, determination of parameters of genetic variation and combining ability based on statistical analysis of phenotypic manifestation of traits still remains effective in practical plant breeding (Zhang et al., 2015; Oliveira et al., 2016; de Pelegrin et al., 2020). There are many publications that reported the results of evaluation of gene action and combining ability in very different crops. For example in rice (Ambikabathy et al., 2021; Del Águila & da Silva, 2021; Gaballah et al., 2022), maize (Yu et al., 2020; Coelho, 2021; Sabitha et al., 2021), sweet corn (Khan et al., 2020), cowpea (Owusu et al., 2020), papaya (Vettorazzi et al., 2021), cotton (Giri et al., 2021; Mudhalvan et al., 2021), eggplants (Datta et al., 2021), groundnut (Daudi et al., 2021), common bean (Nkhata et al., 2021).

The experimental data from systemic crosses are valuable not only for cross-pollinated crops. This is also confirmed by many articles that concur about assessment of the gene action and combining ability for different important traits in bread wheat (Ljubičić et al., 2017; Ayoob, 2020; Abro et al., 2021). Yield and its components under heat and drought-stressed and non-stressed conditions were elucidated (Mwadzingeni et al., 2018; Kamara et al., 2021; Semahegn et al., 2021), under irrigated and rainfed environments (Gupta et al., 2017; Saeed & Khalil, 2017), through several different ecological environments (Sharma et al., 2019), as well as some other morpho-physiological traits (Mohamed, 2019; Ahmad et al., 2020), heat tolerance (Jat et al., 2016), and cellular thermotolerance (El-Rawy et al., 2018). Such a study was conducted in durum wheat (Bajaniya et al., 2019).

There are a number of publications that reported about estimation of combining ability and gene action for different traits in spring (Kumari et al., 2020; Darabad et al., 2021a) and winter (Ciulca et al., 2015; Bernhard et al., 2017) barley. There are articles dedicated to study of grain yield and its components in barley under relatively normal (Panwar & Sharma, 2019; Katiyar et al., 2021; Zymogliad et al., 2021) and stress condition, such as drought (Sultan et al., 2016), salinity (Mansour et al., 2016), nitrogen (Abdel-Moneam & Leilah, 2018), as well as assesment of genetic control of the "seedlings-earing" interphase period (Vashchenko & Shevchenko, 2021). There is also a study of combing ability in six-rowed barley (*Hordeum vulgare* L.) (Lal et al., 2018). In our previous research we revealed genetic capacity in most experimental genotypes for their further breeding improvement by matching the parental components of crossing with complementary effects of GCA, gene effects that increase the individual traits, and combination of the former and latter (Hudzenko, 2017). The results obtained are evidence of the suitability of further such studies to solve some theoretical and applied problems in plant breeding, in particular, identification of patterns of variability (or relative stability) of certain traits in specific environmental conditions, as well as selection of parental components or combinations of crosses with their appropriate manifestation level of the traits under different conditions (years) of research. The constant accumulation of experimental data of breeding and genetic peculiarities of genotypes and traits under exogenous fluctuations of growing conditions will make it possible to predict the response in norm of reaction of a relatively stable genotype by phenotypically labile quantitative traits. Thus, nowadays, both modern (genomic, phenomic, etc.) and "classical" (gene action, combining ability, etc.) breeding and genetic approaches can be used for prediction of hybrid performance.

Reports devoted to the investigation of parameters of genetic variation for yield-related traits in barley differ in their experimental data depending on the genotypes involved in the crossing and the environmental conditions of the trial (Madić et al., 2014; Patial et al., 2016; Jalata et al, 2019). Manifestation level of barley productive tillering, as well as the other yield-related quantitative traits is determined by the action of many different genes (Xu et al., 2018), but it is also largely modified by environmental conditions (Russu et al., 2019; Rodrigues et al., 2020; Hu et al., 2021). These aspects significantly complicate the effectiveness of evaluation and selection of desirable individuals in the splitting populations. In the present study the distribution of crossing combinations according to the indicator of degree of phenotypic dominance showed the prevalence of positive overdominance in Scheme I in 2020 and in Scheme II in both years. In Scheme I in 2019 most of the combinations had intermediate inheritance. Along with that, one should note the differences in the percent of combinations with the different mode of the inheritance of productive tillering in different crossing schemes and their variability over the years. Thus, the degree of phenotypic dominance significantly varied depending on both varieties involved in crossing schemes and conditions of the years of trials. It is important for the breeder to identify combinations with a relatively stable manifestation of overdominance. Positive overdominance is closely related with heterosis. Heterosis is the increased vigour of growth, survival, fertility, and productivity of hybrids, as composed with the two homozygotes (Li et al., 2021). It is a result from crosses between two genetically different parental components and is usually associated with increased heterozygosity. The high degree of heterosis is very valuable for commercial production of F_1 (Yang et al., 2022). However, it is also important for developing varieties. We found that in combinations with a high heterosis in F_1 in the next splitting generations a higher frequency of transgressions may emerge. The challenge for the breeder is to identify such individuals by testing hybrid combinations in a several generations. In Scheme I we observed the overdominance in both years only in four hybrid combinations MIP Tytul / Beatrix, Beatrix / MIP Tytul, Beatrix / Gladys, and Datcha / MIP Tytul. It should be noted that combinations with positive dominance in both years (Beatrix / Avhur) or ones with shift from positive dominance to overdominance (Quench / Beatrix) can also be valuable in practical breeding to increase the level of manifestation of the trait. In Scheme II the overdominance in both years was revealed in seven hybrid combinations Kozyr / Condor, Condor / Kozyr, Condor / Vitrazh, Condor / MIP Myroslav, Sebastian / MIP Myroslav, MIP Myroslav / Kozyr, and MIP Myroslav / Condor. In Scheme II, as compared to Scheme I, no combinations were found with positive dominance in both years. At the same time, there were six hybrid combinations with shift from positive dominance to positive overdominance (Condor / Sebastian, Sebastian / Vitrazh, Sebastian / CDC Rattan, CDC Rattan / Sebastian, MIP Myroslav / Sebastian, and MIP Myroslav / CDC Rattan). The above mentioned hybrid combinations have a practical value for further selection to increase the trait.

We established significant differences in the gene action for productive tillering among the varieties involved in crossings. In Scheme I, the negative values of the coefficient of correlation of the sum of covariance and variance and the mean value of the trait indicated that in both years the dominance was mainly unidirectional and due to dominant effects. Thus, in hybrid populations of Scheme I the final selection for high productive tillering will be effective in later generations, when dominant alleles become homozygous. Along with that, in Scheme II in both years the values of the indicator of direction of dominance were not reliable and it pointed to multidirectional dominance. Thus, in the Scheme II it is theoretically possible to select plants with high productive tillering on both recessive and dominant basis. With the graphical regression analysis we revealed that in Scheme I in 2019 the trait was mainly controlled by the additive-dominant system, but in 2020 there was a strong manifestation of complementary epistasis. Epistasis is the nonreciprocal interaction of nonallelic genes in which one gene interferes with the phenotypic expression of another gene so that the phenotype is determined effectively by the former (Schlegel, 2003). Epistasis complicates the characterization of the parental components involved in the crossing by the parameters of genetic variation. At the same time, the presence of epistasis makes it possible to identify and select promising genotypes with relatively "new" gene action that determined the phenotypic manifestation of the trait. However, this requires testing a significant quantity of plant material in the splitting generations.

The coefficient of heritability is widely used for calculation of the genetically determined part in the general phenotypic variation of different traits (Darabad et al., 2021b). Heritability is a ratio of variance due to genes with additive effects and the phenotypic variance. In the other words, it is a measure of the degree to which a phenotype is genetically determined and can be changed by selection. In the studies by various authors in barley the coefficient of heritability in the broad sense varied from 0.22 for peduncle length to 0.57 for thousand kernel weight (Dinsa et al., 2018), from 0.50 for grain yield to 0.98 for kernel number per spike and thousand kernel weight (Marzougui & Chargui, 2018; Ali & Sayed, 2019; Sayd et al., 2019), from 0.24 for grain yield to 0.96 for kernel number for spike (Ahmadi et al., 2016). Several reports showed that for productive tillering in barley the coefficient of heritability in a broad sense varied from low (0.22) (Matin et al., 2019) to high (0.70–0.89) (Kumar et al., 2013; Yadav et al., 2015), and the coefficient of heritability in a narrow sense varied from 0.14 to 0.42 (Malik et al., 2018; Habouh, 2019). We revealed high values of the coefficient of heritability in a broad sense in both schemes (H_{bs} = 0.84–0.94). The coefficient of heritability in a narrow sense had lower numerical value (h_{ns} = 0.41–0.65). The difference between the coefficients of heritability in broad and in narrow sense indicated a significant impact of non-additive effects on the level of manifestation of productive tillering. At the same time, such level of heritability in the narrow sense makes possible the successful selection of individuals with genetically determined increased productive tillering in the splitting generations.

Thus, in general, the degree of phenotypic dominance, parameters of genetic variation and coefficient of heritability showed very complex gene action for productive tillering in barley and significant role non-genetic factors in phenotypic manifestation of the trait.

General combining ability is the average performance of a parental component in series of crosses. The most promising genotypes for creation a new initial breeding material are ones with high effects of GCA under different growing conditions (Fasahat et al., 2016). In Scheme I in both years only the varieties Beatrix and Datcha had significant high effects of GCA for productive tillering. In Scheme II the varieties MIP Myroslav and Kozyr were relatively better in terms of the effects of GCA in comparison to other ones. On the whole, the results of our in-depth evaluation of gene action for productive tillering in F_1 of spring barley showed that the maximal trait improvement could be achieved in crossings with spring barley varieties Beatrix, Datcha, MIP Myroslav, and Kozyr.

Conclusion

In our study we revealed gene action and combining ability for productive tillering in spring barley varieties of different origin, purposes of usage and botanical affiliation. The degree of phenotypic dominance significantly varied depending on both varieties involved in crossing schemes and conditions of the years of trials. There was overdominance in loci in both schemes in both years. The other parameters of genetic variation showed significant differences in the gene action for productive tillering among the genotypes involved in crossing. In the crossing scheme with only elite malting barley varieties (Scheme I) the negative values of the coefficient of correlation between the sum of covariance and variance and the mean value of the trait indicated that in both years the dominance was mainly unidirectional and due to dominant effects. Vice versa, when different botanical varieties were involved in crosses (Scheme II) in both years the values of the indicator of direction of dominance were not reliable and they pointed to multidirectional dominance. In Scheme I compliance with the additive-dominant system and overdominance in loci were revealed in one year, but in the another year there was a strong epistasis. In Scheme II in both years the non-allelic interaction was identified. In general, the degree of phenotypic dominance, parameters of genetic variation and coefficient of heritability showed very complex gene action for productive tillering in barley and the significant role of non-genetic factors in phenotypic manifestation of the trait. Despite this, the level of heritability in the narrow sense in both schemes pointed to the possibility of the successful selection of individuals with genetically determined increased productive tillering in the splitting generations. In Scheme I the final selection for productive tillering will be more effective in later generations, when dominant alleles become homozygous. In Scheme II it is theoretically possible to select plants with high productive tillering on both recessive and dominant basis. In both schemes the non-allelic interaction should be taken into consideration. Spring barley varieties Beatrix, Datcha, MIP Myroslav, and Kozyr can be used as effective genetic sources for involvement in crossings aimed to improve the productive tillering.

References

Abdel-Ghani, A. H., Sharma, R., Wabila, C., Dhanagond, S., Owais, S. J., Duwayri, M. A., Al-Dalain, S. A., Klukas, C., Chen, D., Lübberstedt, T., von Wirén, N., Graner, A., Kilian, B., & Neumann, K. (2019). Genome-wide association mapping in a diverse spring barley collection reveals the presence of QTL hotspots and candidate genes for root and shoot architecture traits at seedling stage. BMC Plant Biology, 19, 216.

Abdel-Moneam, M. A., & Leilah, A. A. A. (2018). Combining ability for yield and its attributes in barley under stressed and non-stressed nitrogen fertilization environments. International Journal of Advanced Research in Biological Sciences, 5(3), 37–50.

Abro, T. F., Rajput, A. A., Sootaher, J. K., Shar, P. A., Chang, M. S., Naeem, M., Siyal, A. L., Siyal, F. H., Menghwar, K. K., Baloch, A., Keerio, A., & Vistro, M. A. (2021). Estimation of combining ability in F_2 hybrids of bread wheat (*Triticum aestivum* L.) genotypes: GCA and SCA effects of F_2 hybrids in bread wheat. Proceedings of the Pakistan Academy of Sciences: B. Life and Environmental Sciences, 58(2), 69–81.

Ahmad, I., Mohammad, F., Jadoon, S. A., Zeb, A., Munsif, F., & Ahmad, W. (2020). Diallel analysis for the inheritance study of phytic acid along with morpho-yield traits in bread wheat. African Journal of Biotechnology, 19(5), 259–264.

Ahmadi, J., Vaezi, B., & Pour-Aboughadareh, A. (2016). Analysis of variability, heritability, and interrelationships among grain yield and related characters in barley advanced lines. Genetika, 48(1), 73–85.

Ali, M. B., & Sayed, M. A. (2019). Stability analyses and heritability of a doubled haploid population of barley (*Hordeum vulgare* L.). Egyptian Journal of Agronomy, 41(1), 47–58.

Alqudah, A. M., Koppolu, R., Wolde, G. M., Graner, A., & Schnurbusch, T. (2016). The genetic architecture of barley plant stature. Frontiers in Genetics, 7, 117.

Ambikabathy, A., Banumathy, S., Gnanamalar, R. P., Arunchalam, P., Jeyaprakash, P., Amutha, R., & Venkatraman, N. S. (2021). Studies on combining ability and heterosis for yield and drought tolerance traits in rice (*Oryza sativa* L.). Electronic Journal of Plant Breeding, 12(4), 1292–1299.

Ansarifar, J., Akhavizadegan, F., & Wang, L. (2020). Performance prediction of crosses in plant breeding through genotype by environment interactions. Scientific Reports, 10, 11533.

Assefa, A., Girmay, G., Alemayehu, T., & Lakew, A. (2021). Performance evaluation and stability analysis of malt barley (*Hordeum vulgare* L.) varieties for yield and quality traits in Eastern Amhara, Ethiopia. CABI Agriculture and Bioscience, 2, 31.

Ayoob, M. H. (2020). Combining ability analysis, estimation of heterosis and some genetic parameters using half diallel cross in bread wheat (*Triticum aestivum* L.). Journal of Education and Science, 29(1), 96–103.

Babb, S., & Muehlbauer, G. J. (2003). Genetic and morphological characterization of the barley uniculm2 (cul2) mutant. Theoretical and Applied Genetics, 106(5), 846–857.

Bai, Y., Zhao, X., Yao, X., Yao, Y., An, L., Li, X., Wang, Y., Gao, X., Jia, Y., Guan, L., Li, M., Wu, K., & Wang, Z. (2021). Genome wide association study of plant height and tiller number in hulless barley. PLoS One, 16(12), e0260723.

Bajaniya, N. A., Pansuriya, A. G., Vekaria, D. M., Singh, C., & Savaliya, J. J. (2019). Combining ability analysis for grain yield and its components in durum wheat (*Triticum durum* Desf.). Indian Journal of Pure and Applied Biosciences, 7(4), 217–224.

Bauer, B., & von Wirén, N. (2020). Modulating tiller formation in cereal crops by the signalling function of fertilizer nitrogen forms. Scientific Reports, 10, 20504.

Beil, G. M., & Atkins, R. E. (1965). Inheritance of quantitative characters in grain Sorghum. Iowa State Journal of Science, 39(3), 139–158.

Bernhard, T., Wolfgang, F., Voss-Fels, K. P., Frisch, M., Snowdon, R. J., & Wittkop, B. (2017). Heterosis for biomass and grain yield facilitates breeding of productive dual-purpose winter barley hybrids. Crop Science, 57(5), 2405–2418.

Bohačenko, I., Psota, V., Hartmann, J., & Musilova, M. (2021). Combining effect of high temperature and drought on yield and malting quality of barley. Czech Journal of Food Sciences, 39(1), 17–22.

Ciulca, A. C., Madosa, E., Velicevici, G., & Ciulca, S. (2015). Combining ability for some grains morphological traits in winter barley. Journal of Horticulture, Forestry and Biotechnology, 19(3), 67–72.

Coelho, I. F., Peixoto, M. A., Marçal, T. S., Bernardeli, A., Silva Alves, R., de Lima, R. O., dos Reis, E. F., & Bhering, L. L. (2021) Accounting for spatial trends in multienvironment diallel analysis in maize breeding. PLoS One, 16(10), e0258473.

Cui, Y., Li, R., Li, G., Zhang, F., Zhu, T., Zhang, Q., Ali, J., Li, Z., & Xu, S. (2020). Hybrid breeding of rice via genomic selection. Plant Biotechnology Journal, 18(1), 57–67.

Dabbert, T., Okagaki R. J., Cho, S., Boddu, J., & Muehlbauer, G. J. (2009). The genetics of barley low-tillering mutants: Absent lower laterals (als). Theoretical and Applied Genetics, 118(7), 1351–1360.

Dabbert, T., Okagaki, R. J., Cho, S., Heinen, S., Boddu, J., & Muehlbauer, G. J. (2010). The genetics of barley low-tillering mutants: Low number of tillers-1 (lnt1). Theoretical and Applied Genetics, 121(4), 705–715.

Darabad, J. R., Rashidi, V., Shahbazi, H., Vahed, M. M., & Khalilvand, E. (2021a). Genetic analysis of agronomic traits of barley (*Hordeum vulgare* L.) cultivars under salinity stress using diallel cross. Plant Genetic Researches, 7(2), 83–96.

Darabad, J. R., Rashidi, V., Shahbazi, H., Vahed, M. M., & Khalilvand, E. (2021b). Heritability and genetic parameters of some antioxidant enzyme activities in barley (*Hordeum vulgare* L.) cultivars under salinity stress. Tarim Bilimleri Dergisi, 27(2), 187–194.

Datta, D. R., Rafii, M. Y., Misran, A., Jusoh, M., Yusuff, O., Haque, M. A., & Jatto, M. I. (2021). Half diallel analysis for biochemical and morphological traits in cultivated eggplants (*Solanum melongena* L.). Agronomy, 11(9), 1769.

Daudi, H., Shimelis, H., Mathew, I., Rathore, A., & Ojiewo, C. (2021). Combining ability and gene action controlling rust resistance in groundnut (*Arachis hypogaea* L.). Scientific Reports, 11, 16513.

de Pelegrin, A. J., Nardino, M., Carvalho, I. R., Szareski, V. J., Ferrari, M., Conte, G. G., de Oliveira, A. C., de Souza, V. Q., & da Maia, L. C. (2020). Combining ability as a criterion for wheat parents selection. Functional Plant Breeding Journal, 2(1), 4.

Del Águila, R. M., & da Silva, E. F. (2021). Efficiency of crosses selection for yield in red rice through diallel analysis. Agronomy Science and Biotechnology, 7, 1–10.

Dinsa, T., Mekbib, F., & Letta, T. (2018). Genetic variability, heritability and genetic advance of yield and yield related traits of food barley (*Hordeum vulgare* L.) genotypes in Mid Rift Valley of Ethiopia. Advances in Crop Science and Technology, 6(5), 1000401.

Dockter, C., Gruszka, D., Braumann, I., Druka, A., Druka, I., Franckowiak, J., Gough, S. P., Janeczko, A., Kurowska, M., Lundqvist, J., Lundqvist, U., Marzec, M., Matyszczak, I., Müller, A. H., Oklestkova, J., Schulz, B., Zakhrabekova, S., & Hansson, M. (2014). Induced variations in brassinosteroid genes define barley height and sturdiness, and expand the green revolution genetic toolkit. Plant Physiology, 166(4), 1912–1927.

Druka, A., Franckowiak, J., Lundqvist, U., Bonar, N., Alexander, J., Houston, K., Radovic, S., Shahinnia, F., Vendramin, V., Morgante, M., Stein, N., & Waugh, R. (2011). Genetic dissection of barley morphology and development. Plant Physiology, 155(2), 617–627.

Edney, M. J., MacLeod, A. L., & LaBerge, D. E. (2014). Evolution of a quality testing program for improving malting barley in Canada. Canadian Journal of Plant Science, 94(3), 535–544.

El-Rawy, M. A., Hassan, M. I., Omran, M. F., & El-defrawy, M. M. (2018). Gene action and combining ability of cellular thermotolerance in bread wheat (*Triticum aestivum* L.). Plant Breeding and Biotechnology, 6(3), 206–220.

Fang, Y., Zhang, X., & Xue, D. (2019). Genetic analysis and molecular breeding applications of malting quality QTLs in barley. Frontiers in Genetics, 10, 352.

Fasahat, P., Rajabi, A., Rad, J. M., & Derera, J. (2016). Principles and utilization of combining ability in plant breeding. Biometrics and Biostatistics International Journal, 4(1), 1–22.

Fonseca, J. M. O., Klein, P. E., Crossa, J., Pacheco, A., Perez-Rodriguez, P., Ramasamy, P., Klein, R., & Rooney, W. L. (2021). Assessing combining abilities, genomic data, and genotype x environment interactions to predict hybrid grain sorghum performance. The Plant Genome, 14(3), e20127.

Franckowiak, J. D., & Lundqvist, U. (2013). Descriptions of barley genetic stocks. Barley Genetics Newsletter, 43, 48–223.

Gaballah, M. M., Attia, K. A., Ghoneim, A. M., Khan, N., EL-Ezz, A.F., Yang, B., Xiao, L., Ibrahim, E. I., & Al-Doss, A. A. (2022). Assessment of genetic parameters and gene action associated with heterosis for enhancing yield characters in novel hybrid rice parental lines. Plants, 11(3), 266.

Gamayunova, V. V., Kasatkina, T. O., & Baklanova, T. V. (2021). Agroeconomic assessment of utilization biologics in the cultivation of spring barley in the conditions of the Southern Steppe of Ukraine. Agrology, 4(2), 65–70.

Giri, R. K., Verma, S. K., & Yadav, J. P. (2021). Study of heterosis, combining ability and parental diversity for seed cotton yield and contributing traits using diallel data in cotton (*G. hirsutum* L.). Indian Journal of Agricultural Research, 55(5), 556–562.

Govindaraju, D. R. (2019). An elucidation of over a century old enigma in genetics – heterosis. PLoS Biology, 17(4), e3000215.

Griffing, B. (1956a). Concept of general and specific combining ability in relation to diallel crossing system. Australian Journal of Biological Sciences, 9(4), 463–493.

Griffing, B. (1956b). A generalised treatment of the use of diallel crosses in quantitative inheritance. Heredity, 10(1), 31–50.

Guo, X., Sarup, P., Jensen, J. D., Orabi, J., Kristensen, N. H., Mulder, F. A. A., Jahoor, A., & Jensen, J. (2020). Genetic variance of metabolomic features and their relationship with malting quality traits in spring barley. Frontiers in Plant Science, 11, 575467.

Gupta, V. K., Agarwal, A. P., & Minz, M. G. (2017). Combining ability analysis for yield and its component traits in wheat (*Titicum aestivum* L.) under timely sown irrigated condition. International Journal of Bio-Resource and Stress Management, 8(6), 784–789.

Haaning, A. M., Smith, K. P., Brown-Guedira, G. L., Chao, S., Tyagi, P., & Muehlbauer, G. J. (2020). Natural genetic variation underlying tiller development in barley (*Hordeum vulgare* L). G3: Genes, Genomes, Genetics, 10(4), 1197–1212.

Habiyaremye, C., Schroeder, K. L., Reganold, J. P., White, D., Packer, D., & Murphy, K. M. (2021). Effect of nitrogen and seeding rate on ß-glucan, protein, and grain yield of naked food barley in no-till cropping systems in the Palouse Region of the Pacific Northwest. Frontiers in Sustainable Food Systems, 5, 663445.

Habouh, M. A. F. (2019). Inheritance of plant height, grain yield and its components in three barley crosses. Journal of Plant Production, 10(3), 293–297.

Habschied, K., Lalić, A., Krstanović, V., Dvojković, K., Abičić, I., Šimić, G., & Mastanjević, K. (2021). Comprehensive comparative study of the malting qualities of winter hull-less and hulled barley (2016–2019). Fermentation, 7(1), 8.

Hayman, B. I. (1954). The theory and analysis of diallel crosses. Genetics, 39(6), 789–809.

Hayman, B. I. (1958). The theory and analysis of diallel crosses. II. Genetics, 43(1), 63–85.

Hayman, B. I. (1960). The theory and analysis of diallel crosses. III. Genetics, 45(2), 155–172.

He, J., Shao, G., Wei, X., Huang, F., Sheng, Z., Tang, S., & Hu, P. (2017). Fine mapping and candidate gene analysis of qTAC8, a major quantitative trait locus controlling tiller angle in rice (*Oryza sativa* L.). PLoS One, 12(5), e0178177.

Hu, Y., Barmeier, G., & Schmidhalter, U. (2021). Genetic variation in grain yield and quality traits of spring malting barley. Agronomy, 11(6), 1177.

Hudzenko, V. M. (2017). Dialelnyi analiz produktyvnoho kushchinnia u suchasnykh sortiv yachmeniu yaroho [Diallel analysis of productive tiller number in modern spring barley varieties]. Scientific Reports of NULES of Ukraine, 5, 69 (in Ukrainian).

Hussien, A., Tavakol, E., Horner, D. S., Muñoz-Amatriaín, M., Muehlbauer, G. J., & Rossini, L. (2014). Genetics of tillering in rice and barley. The Plant Genome, 7(1), 1–20.

Ishchenko, V. A., & Kozelets, H. M. (2021). Formation of spring barley productivity depending on seed inoculation with a biopreparation and foliar fertilization in the Steppe of Ukraine. Agrology, 4(4), 180–186.

Jalata, Z., Mekbib, F., Lakew, B., & Ahmed, S. (2019). Gene action and combining ability test for some agro-morphological traits in barley. Journal of Applied Sciences, 19(2), 88–95.

Jarquin, D., de Leon, N., Romay, C., Bohn, M., Buckler, E. S., Ciampitti, I., Edwards, J., Ertl, D., Flint-Garcia, S., Gore, M. A., Graham, C., Hirsch, C. N., Holland, J. B., Hooker, D., Kaeppler, S. M., Knoll, J., Lee, E. C., Lawrence-Dill, C. J., Lynch, J. P., Moose, S. P., Murray, S. C., Nelson, R., Rocheford, T., Schnable, J. C., Schnable, P. S., Smith, M., Springer, N., Thomison, P., Tuinstra, M., Wisser, R. J., Xu, W., Yu, J., & Lorenz, A. (2021). Utility of climatic information via combining ability models to improve genomic prediction for yield within the genomes to fields maize project. Frontiers in Genetics, 11, 592769.

Jat, B. S., Bharti, B., Ranwah, B. R., & Khan, S. (2016). Combining ability studies for heat tolerance traits in bread wheat [*Triticum aestivum* (L.) em. Thell]. Electronic Journal of Plant Breeding, 7(4), 996–1001.

Jia, Q., Zhang, X. Q., Westcott, S., Broughton, S., Cakir, M., Yang, J., Lance, R., & Li, C. (2011). Expression level of a gibberellin 20-oxidase gene is associated with multiple agronomic and quality traits in barley. Theoretical and Applied Genetics, 122(8), 1451–1460.

Kamara, M. M., Ibrahim, K. M., Mansour, E., Kheir, A. M. S., Germoush, M. O., Abd El-Moneim, D., Motawei, M. I., Alhusays, A. Y., Farid, M. A., & Rehan, M. (2021). Combining ability and gene action controlling grain yield and its related traits in bread wheat under heat stress and normal conditions. Agronomy, 11(8), 1450.

Kassie, M. M., Awoke, Y., & Demesie, Z. (2018). Evaluation of malt barley (*Hordeum distichon* L.) genotypes for grain yield and malting quality parameters at Koga irrigation in Western Amhara Region. International Journal of Plant Breeding and Genetics, 12(1), 13–18.

Katiyar, A., Sharma, A., Singh, S., Srivastava, A., & Vishwakarma, S. R. (2021). Combining ability analysis for yield traits in barley (*Hordeum vulgare* L.). Electronic Journal of Plant Breeding, 12(2), 583–588.

Khan, A., Ur-Rahman, H., Ahmad, A., Iqbal, M., Kamal, S., Khan, S., & Bu, J. (2020). Combining ability analysis in sweet corn (*Zea mays saccharrata* L.) using line by tester design. Advances in Food Technology and Nutritional Sciences, 6(2), 47–52.

Kompanets, K. V., & Kozachenko, M. R. (2017). Selektsijna tsinnist ta efektyvnist vykorystannia v selektsiji bezostykh ta ostystykh sortiv yachmeniu yaroho [Breeding value and efficiency of use of awny and awnless barley cultivars in breeding]. Plant Breeding and Seed Production, 112, 56–67 (in Ukrainian).

Kong, W., Guo, H., Goff, V. H., Lee, T. H., Kim, C., & Paterson, A. H. (2014). Genetic analysis of vegetative branching in sorghum. Theoretical and Applied Genetics, 127(11), 2387–2403.

Koprna, R., Humplík, J. F., Špíšek, Z., Bryksová, M., Zatloukal, M., Mik, V., Novák, O., Nisler, J., & Doležal, K. (2021). Improvement of tillering and grain yield by application of cytokinin derivatives in wheat and barley. Agronomy, 11(1), 67.

Kumar, M., Vishwakarma, S. R., Bhushan, B., & Kumar, A. (2013). Estimation of genetic parameters and character association in barley (*Hordeum vulgare* L.). Journal of Wheat Research, 5(2), 76–78.

Kumari, A., Vishwakarma, S. R., & Singh, Y. (2020). Evaluation of combining ability and gene action in barley (*Hordeum vulgare* L.) using Line x Tester analysis. Electronic Journal of Plant Breeding, 11(1), 97–102.

Labroo, M. R., Ali, J., Aslam, M. U., de Asis, E. J., dela Paz, M. A., Sevilla, M. A., Lipka, A. E., Studer, A. J., & Rutkoski, J. E. (2021). Genomic prediction of yield traits in single-cross hybrid rice (*Oryza sativa* L.). Frontiers in Genetics, 12, 692870.

Laidig, F., Piepo, H.-P., Rentel, D., & Meyer, U. (2017). Breeding progress, genotypic and environmental variation and correlation of quality traits in malting barley in German official variety trials between 1983 and 2015. Theoretical and Applied Genetics, 130(11), 2411–2429.

Lal, C., Shekhawat, A. S., Rajput, S. S., Singh, J., & Sharma, S. R. (2018). Combining ability analysis for grain yield and its attributing traits in six-rowed barley (*Hordeum vulgare* L.). International Journal of Pure and Applied Bioscience, 6(4), 408–414.

Li, D., Zhou, Z., Lu, X., Jiang, Y., Li, G., Li, J., Wang, H., Chen, S., Li, X., Würschum, T., Reif, J. C., Xu, S., Li, M., & Liu, W. (2021). Genetic dissection of hybrid performance and heterosis for yield-related traits in maize. Frontiersin Plant Science, 12, 774478.

Li, Z., Lhundrup, N., Guo, G., Dol, K., Chen, P., Gao, L., Chemi, W., Zhang, J., Wang, J., Nyema, T., Dawa, D., & Li, H. (2020). Characterization of genetic diversity and genome-wide association mapping of three agronomic traits in qingke barley (*Hordeum vulgare* L.) in the Qinghai-Tibet Plateau. Frontiers in Genetics, 11, 638.

Li, Z., Philipp, N., Spiller, M., Stiewe, G., Reif, J. C., & Zhao, Y. (2016). Genome-wide prediction of the performance of three-way hybrids in barley. The Plant Genome, 10(1), 1–9.

Liller, C. B., Neuhaus, R., von Korff, M., Koornneef, M., & van Esse, W. (2015). Mutations in barley row type genes have pleiotropic effects on shoot branching. PLoS One, 10(10), e0140246.

Liu, J., Luo, W., Qin, N., Ding, P., Zhang, H., Yang, C., Mu, Y., Tang, H., Liu, Y., Li, W., Jiang, Q., Ghen, G., Wei, Y., Zheng, Y., Liu, C., Lan, X., & Ma, J. (2018). A 55 K SNP array-based genetic map and its utilization in QTL mapping for productive tiller number in common wheat. Theoretical and Applied Genetics, 131(11), 2439–2450.

Ljubičić, N., Petrović, S., Kostić, M., Dimitrijević, M., Hristov, N., Kondić-Špika, A., & Jevtić, R. (2017). Diallel analysis of some important grain yield traits in bread wheat crosses. Turkish Journal of Field Crops, 22(1), 1–7.

Madić, M. R., Djurović, D. S., Knezevi, D. S., Paunović, A. S., & Tanaskovic, S. T. (2014). Combining abilities for spike traits in a diallel cross of barley. Journal of Central Europran Agriculture, 15(1), 108–116.

Malik, P., Singh, S. K., Singh, L., Gupta, P. K., Kumar, S., Yadav, R. K., Amardeep, & Kumar, A. (2018). Studies on genetic heritability and genetic advance for seed yield and its component in barley (*Hordeum vulgare* L.). International Journal of Pure and Applied Bioscience, 6(6), 810–813.

Mansour, E., & Moustafa, E. S. A. (2016). Estimation of combining ability and genetic components for yield contributing traits in spring barley under normal and salinity conditions. Egyptian Journal of Agronomy, 38(3), 431–483.

Marzec, M., Gruszka, D., Tylec, P., & Szarejko, I. (2016). Identification and functional analysis of the HvD14 gene involved in strigolactone signaling in *Hordeum vulgare*. Physiologia Plantarum, 158(3), 341–355.

Marzougui, S., & Chargui, A. (2018). Estimation of correlation, regression and heritability among barley (*Hordeum vulgare* L.) accessions. Journal of New Sciences, Agriculture and Biotechnology, 60(2), 3838–3843.

Mastanjević, K., Lenart, L., Šimić, G., Lalić, A., & Krstanović, V. (2017). Malting quality indicators of Croatian dual-purpose barley varieties. Croatian Journal of Food Science and Technology, 9(2), 145–151.

Matin, M. Q. I., Amiruzzaman, M., Billah, M. M., Banu, M. B., Naher, N., & Choudhury, D. A. (2019). Genetic variability and path analysis studies in barley (*Hordeum vulgare* L.). International Journal of Applied Sciences and Biotechnology, 7(2), 243–247.

Matthies, I. E., Malosetti, M., Röder, M. S., & van Eeuwijk, F. (2014). Genome-wide association mapping for kernel and malting quality traits using historical European barley records. PLoS One, 9(11), e110046.

Mohamed, B. A. (2019). Combining ability of physiological and yield traits of bread wheat diallel crosses under timely and late sowing dates. Egyptian Journal of Agronomy, 41(2), 159–181.

Mudhalvan, S., Rajeswari, S., Mahalingam, L., Jeyakumar, P., Muthuswami, M., & Premalatha, N. (2021). Combining ability estimates and heterosis analysis on major yield attributing traits and lint quality in American cotton (*Gossypium hirsutum* L.). Electronic Journal of Plant Breeding, 12(4), 1111–1119.

Mwadzingeni, L., Shimelis, H., & Tsilo, T. J. (2018). Combining ability and gene action controlling yield and yield components in bread wheat (*Triticum aestivum* L.) under drought-stressed and non-stressed conditions. Plant Breeding, 137(4), 502–513.

Nadolska-Orczyk, A., Rajchel, I. K., Orczyk, W., & Gasparis, S. (2017). Major genes determining yield-related traits in wheat and barley. Theoretical and Applied Genetics, 130(6), 1081–1098.

Narwal, S., Kumar, D., Sheoran, S., Verma, R. P. S., & Gupta, R. K. (2017). Hulless barley as a promising source to improve the nutritional quality of wheat products. Journal of Food Science and Technology, 54(9), 2638–2644.

Naumov, O. G., Kozachenko, M. R., Vasko, N. I., Solonechnii, P. M., & Vazhenina, O. E. (2014). Selektsiia waxy-iachmeniu [Waxy barley breeding]. Plant Breeding and Seed Production, 105, 60–69 (in Ukrainian).

Naz, A. A., Arifuzzaman, M., Muzammil, S., Pillen, K., & Léon, J. (2014). Wild barley introgression lines revealed novel QTL alleles for root and related shoot traits in the cultivated barley (*Hordeum vulgare* L.). BMC Genetics, 15, 107.

Nice, L. M., Steffenson, B. J., Blake, T., Horsley, R., Smith, K., & Muehlbauer, G. J. (2017). Mapping agronomic traits in a wild barley advanced backcross-nested association mapping population. Crop Science, 57(3), 1199–1210.

Nkhata, W., Shimelis, H., Melis, R., Chirwa, R., Mzengeza, T., Mathew, I., & Shayanowako, A. (2021). Combining ability analysis of common bean (*Phaseolus vulgaris* L) genotypes for resistance to bean fly (*Ophiomyia* spp.), and grain yield and component traits. Euphytica, 217(5), 93.

Okagaki, R. J., Cho, S., Kruger, W. M., Xu, W. W., Heinen, S., & Muehlbauer, G. J. (2013). The barley UNICULM2 gene resides in a centromeric region and may be associated with signaling and stress responses. Functional and Integrative Genomics, 13(1), 33–41.

Oliveira, G. H. F., Buzinaro, R., Revolti, L. T. M., Giorgenon, C. H. B., Charnai, K., Resende, D., & Moro, G. V. (2016). An accurate prediction of maize crosses using diallel analysis and best linear unbiased predictor (BLUP). Chilean Journal of Agricultural Research, 76(3), 294–299.

Owusu, E. Y., Mohammed, H., Manigben, K. A., Adjebeng-Danquah, J., Kusi, F., Karikari, B., & Sie, E. K. (2020). Diallel analysis and heritability of grain yield, yield components, and maturity traits in cowpea (*Vigna unguiculata* (L.) Walp.). The Scientific World Journal, 2020, 9390287.

Panwar, D., & Sharma, H. (2019). Study of combining ability analysis in barley (*Hordeum vulgare* L.). International Journal of Current Microbiology and Applied Sciences, 8(12), 3004–3011.

Patial, M., Pal, D., & Kumar, J. (2016). Combining ability and gene action studies for grain yield and its component traits in barley (*Hordeum vulgare* L.). SABRAO Journal of Breeding and Genetics, 48(1), 90–96.

Philipp, N., Liu, G., Zhao, Y., He, S., Spiller, M., Stiewe, G., Pillen, K., Reif, J. C., & Li, Z. (2016). Genomic prediction of barley hybrid performance. The Plant Genome, 9(2), 16.

Ramsay, L., Comadran, J., Druka, A., Marshall, D. F., Thomas, W. T. B., MacAulay, M., MacKenzie, K., Simpson, C., Fuller, J., Bonar, N., Hayes, P. M., Lundqvist, U., Franckowiak, J. D., Close, T. J., Muehlbauer, G. J., & Waugh, R. (2011). INTERMEDIUM-C, a modifier of lateral spikelet fertility in barley, is an ortholog of the maize domestication gene TEOSINTE BRANCHED 1. Nature Genetics, 43(2), 169–172.

Rani, M., Singh, G., Siddiqi, R. A., Gill, B. S., Sogi, D. S., & Bhat, M. A. (2021). Comparative quality evaluation of physicochemical, technological, and protein profiling of wheat, rye, and barley cereals. Frontiers in Nutrition, 8, 694679.

Riaz, A., Kanwal, F., Börner, A., Pillen, K., Dai, F., & Alqudah, A. M. (2021). Advances in genomics-based breeding of barley: Molecular tools and genomic databases. Agronomy, 11(5), 894.

Rincent, R., Charpentier, J. P., Faivre-Rampant, P., Paux, E., Le Gouis, J., Bastien, C., & Segura, V. (2018). Phenomic selection is a low-cost and high-throughput method based on indirect predictions: Proof of concept on wheat and poplar. G3: Genes, Genomes, Genetics, 8(12), 3961–3972.

Rodrigues, O., Minella, E., & Costenaro, E. R. (2020). Genetic improvement of barley (*Hordeum vulgare* L.) in Brazil: Yield increase and associated traits. Agricultural Sciences, 11(4), 425–438.

Russu, F., Porumb, I., Mureșanu, F., & Tritean, N. (2019). Estimation of the variability and inheritance of some quantitative traits in two rows spring barley in the conditions of Ards Turda. Romanian Agricultural Research, 36, 67–77.

Sabitha, N., Reddy, D. M., Reddy, D. L., Kumar, M. H., Sudhakar, P., & Reddy, B. R. (2021). Nature of gene action for kernel yield and its component traits in maize (*Zea mays* L.). Electronic Journal of Plant Breeding, 12(4), 1359–1366.

Saeed, M., & Khalil, I. H. (2017). Combining ability and narrow-sense heritability in wheat (*Triticum aestivum* L.) under rainfed environment. Sarhad Journal of Agriculture, 33(1), 22–29.

Sayd, R. M., Amabile, R. F., Faleiro, F. G., Costa, M. C., & Montalvão, A. P. L. (2019). Genetic parameters and agronomic characterization of elite barley accessions under irrigation in the Cerrado. Acta Scientiarum. Agronomy, 41, e42630.

Schlegel, R. H. G. (2003). Encyclopedic dictionary of plant breeding and related subjects. Food Products Press and The Haworth Reference Press, New York, London, Oxford.

Semahegn, Y., Shimelis, H., Laing, M., & Mathew, I. (2021). Combining ability of bread wheat genotypes for yield and yield-related traits under drought-stressed and non-stressed conditions. South African Journal of Plant and Soil, 38(2), 171–179.

Shaaf, S., Bretani, G., Biswas, A., Fontana, I. M., & Rossini, L. (2019). Genetics of barley tiller and leaf development. Journal of Integrative Plant Biology, 61(3), 226–256.

Sharma, V., Dodiya, N. S., Dubey, R. B., Khandagale, S. G., & Khan, R. (2019). Combining ability analysis over environments in bread wheat. Electronic Journal of Plant Breeding, 10(4), 1397–1404.

Shaveta, S., Kaur, H., & Kaur, S. (2019). Hulless barley: A new era of research for food purposes. Journal of Cereal Research, 11(2), 114–124.

Sterna, V., Bleidere, M., Sabovics, M., Auzins, A., Leimane, I., & Krievina, A. (2021). Improving nutritional value of products with flour of the hulless barley cultivar 'Kornelija' as an ingredient. Zemdirbyste - Agriculture, 108(1), 43–50.

Sultan, M. S., Abdel-Moneam, M. A., & Haffez, S. H. (2016). Estimation of combining ability for yield and its components in barley under normal and stress drought condition. Journal of Plant Production, 7(6), 553–558.

Tavakol, E., Okagaki, R., Verderio, G., Shariati, J. V., Hussien, A., Bilgic, H., Scanlon, M. J., Todt, N. R., Close, T. J., Druka, A., Waugh, R., Steuernagel, B., Ariyadasa, R., Himmelbach, A., Stein, N., Muehlbauer, G. J., & Rossini, L. (2015). The barley Uniculme4 gene encodes a blade-on-petiole-like protein that controls tillering and leaf patterning. Plant Physiology, 168(1), 164–174.

Thorwarth, P., Ahlemeyer, J., Bochard, A. M., Krumnacker, K., Blümel, H., Laubach, E., Knöchel, N., Cselényi, L., Ordon, F., & Schmid, K. J. (2017). Genomic prediction ability for yield-related traits in German winter barley elite material. Theoretical and Applied Genetics, 130(8), 1669–1683.

Tokhetova, L. A., Umirzakov, S. I., Nurymova, R. D., Baizhanova, B. K., & Akhmedova, G. B. (2020). Analysis of economic-biological traits of hull-less barley and creation of source material for resistance to environmental stress factors. International Journal of Agronomy, 2020, 8847753.

Vashchenko, V. V., & Shevchenko, A. A. (2021). Variability and genetic control of the "seedlings-earing" interphase period in spring barley under water deficit. Plant Breeding and Seed Production, 119, 94–105.

Vettorazzi, J. C. F., Santa-Catarina, R., Poltronieri, T. P. de S., Cortes, D. F. M., Azevedo, A. O. N., Miranda, D. P., Santana, J. G. S., Ramos, H. C. C., & Pereira, M. G. (2021). Combining ability of recombined F4 papaya lines: A strategy to select hybrid combination. Scientia Agricola, 78(2), e20190191.

Wang, H., Chen, W., Eggert, K., Charnikhova, T., Bouwmeester, H., Schweizer, P., Hajirezaei, M. R., Seiler, C., Sreenivasulu, N., von Wirén, N., & Kuhlmann, M. (2018). Abscisic acid influences tillering by modulation of strigolactones in barley. Journal of Experimental Botany, 69(16), 3883–3898,

Wang, X., Zhang, Z., Xu, Y., Li, P., Zhang, X., & Xu, C. (2020). Using genomic data to improve the estimation of general combining ability based on sparse partial diallel cross designs in maize. The Crop Journal, 8(5), 819–829.

Wang, Z., Liu, Y., Shi, H., Mo, H., Wu, F., Lin, Y., Gao, S., Wang, J., Wei, Y., Liu, C., & Zheng, Y. (2016). Identification and validation of novel low-tiller number QTL in common wheat. Theoretical and Applied Genetics, 129(3), 603–612.

Widener, S., Graef, G., Lipka, A. E., & Jarquin, D. (2021). An assessment of the factors influencing the prediction accuracy of genomic prediction models across multiple environments. Frontiers in Genetics, 12, 689319.

Xu, X., Sharma, R., Tondelli, A., Russell, J., Comadran, J., Schnaithmann, F., Pillen, K., Kilian, B., Cattivelli, L., Thomas, W. T. B., & Flavell, A. J. (2018). Genome-wide association analysis of grain yield-associated traits in a Pan-European barley cultivar collection. The Plant Genome, 11(1), 170073.

Xu, Y., Jia, Q., Zhou, G., Zhang, X. Q., Angessa, T., Broughton, S., Yan, G., Zhang, W., & Li, C. (2017). Characterization of the sdw1 semi-dwarf gene in barley. BMC Plant Biology, 17, 11.

Yadav, R. K., Gautam, S., Palikhey, E., Joshi, B. K., Ghimire, K. H., Gurung, R., Adhikari, A. R., Pudasaini, N., & Dhakal, R. (2018). Agro-morphological diversity of Nepalese naked barley landraces. Agriculture and Food Security, 7, 86.

Yadav, S. K., Singh, A. K., Pandey, P., & Singh, S. (2015). Genetic variability and direct selection criterion for seed yield in segregating generations of barley (*Hordeum vulgare* L.). American Journal of Plant Sciences, 6(9), 1543–1549.

Yang, W., Qin, Z., Sun, H., Hou, Q., Gao, J., Chen, X., Zhang, L., Wang, Y., Zhao, C., & Zhang, F. (2022). Analysis of combining ability for stem-related traits and its correlations with lodging resistance heterosis in hybrid wheat. Journal of Integrative Agriculture, 21(1), 26–35.

Yang, Y., Ferreira, G., Teets, C. L., Corl, B. A., Thomason, W. E., & Griffey C. A. (2018). Effects of feeding hulled and hull-less barley with low- and high-forage diets on lactation performance, nutrient digestibility, and milk fatty acid composition of lactating dairy cows. Journal of Dairy Science, 101(4), 3036–3043.

Yao, X., Wu, K., Yao, Y., Bai, Y., Ye, J., & Chi, D. (2018). Construction of a high-density genetic map: genotyping by sequencing (GBS) to map purple seed coat color (Psc) in hulless barley. Hereditas, 155, 37.

Ye, L., Wang, Y., Long, L., Luo, H., Shen, Q., Broughton, S., Wu, D., Shu, X., Dai, F., Li, C., & Zhang, G. (2019). A trypsin family protein gene controls tillering and leaf shape in barley. Plant Physiology, 181(2), 701–713.

Yu, K., Wang, H., Liu, X., Xu, C., Li, Z., Xu, X., Liu, J., Wang, Z., & Xu, Y. (2020). Large-scale analysis of combining ability and heterosis for development of hybrid maize breeding strategies using diverse germplasm resources. Frontiers in Plant Science, 11, 660.

Yuan, X., Yu, C., Shimojo, M., & Shao, T. (2012). Improvement of fermentation and nutritive quality of straw-grass silage by inclusion of wet hulless-barley distillers' grains in Tibet. Asian-Australasian Journal of Animal Sciences, 25(4), 479–485.

Zhang, X., Lv, L., Lv, C., Guo, B., & Xu, R. (2015). Combining ability of different agronomic traits and yield components in hybrid barley. PloS One, 10(6), 1–9.

Zhu, X., Leiser, W. L., Hahn, V., & Würschum, T. (2021). Phenomic selection is competitive with genomic selection for breeding of complex traits. The Plant Phenome Journal, 4(1), e20027.

Zymogliad, O. V., Kozachenko, M. R., Vasko, N. I., Solonechnyi, P. M., Vazhenina, O. E., & Naumov, O. G. (2021). Performance inheritance and combining ability of spring barley accessions. Plant Breeding and Seed Production, 119, 106–116.