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EINKORN WHEAT TILLERING: MODELS OF INHERITANCE

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ABSTRACT

The need for einkorn wheat breeding improvement is due to its value as a source of healthy nutrition. Tillering is an important agronomic trait determining yield. Genetic analysis of tillering was carried out on reciprocal hybrids between accessions of *T. monococcum* L.: *var. nigricultum* (UA0300311) and *var. monococcum* (UA0300282). It was found that the segregation pattern on this trait depends on vegetation conditions. Segregation in the F_2 of reciprocal crosses indicates effect of two major genes with a series of polygenes which influence the quantitative expression of tillering with different efficiency degrees. The heritability of tillering in reciprocal crosses is of 68-71 % and 84-92 %.

Keywords: Einkorn wheat, hybrid, inheritance, tillering.

INTRODUCTION

Tillering is among an important agronomic traits that determines the architecture of a wheat plant and its potential yield (Ding et al., 2023; Sun et al., 2023). Depending on the ability of shoots to form ears, tillering is labelled as unproductive and productive. The tillering intensity is influenced by the method, timing and density of plant sowing as well as by amount of fertilizer (Li et al., 2007; Zhang et al., 2013; Liu et al., 2023; Xu et al., 2021).

Einkorn wheat is one of the oldest wheat species. Although its cultivation has long ceased on a large scale (Brandolini and Heun, 2019), interest in it as a source of healthy food has recently increased. This is due to the fact that its flour has higher content of vitamins B_1, B_2, B_5, antioxidants, mineral substances and other valuable components compared to bread wheat flour (Serpen et al., 2008; Pehlivan Karakas et al., 2021; Brandolini et al., 2023). It is important to note that einkorn products can be consumed by people with certain types of wheat gluten intolerance (Di Stasio et al., 2020; Picascia et al., 2020).

Einkorn has not been affected by modern breeding, therefore it is low-yielding. One of the traits by which its yield can be increased may be productive tillering of the plants. For successful breeding, information on the genetic control of this trait is needed. There is no information on the inheritance of tillering in einkorn. The aim of this study was to find out type of tillering inheritance in einkorn wheat and heritability of this trait in reciprocal crosses using segregation analysis

MATERIALS AND METHODS

Object of study

The accessions of *Triticum monococcum* L. *var. nigricultum* UA0300311 (Syria) and *var. monococcum* UA0300282 (Hungary) from the collection of the National Bank of Plant Genetic Resources of Ukraine were taken for crossing. The accession UA0300311 is of winter growth habit, has black ear. The accession UA0300282 is of spring growth habit and has light-colored ear (Fig. 1).

Schematic of the genetic experiment

From the pair of reciprocal crosses UA0300311×UA0300282 and UA0300282×UA0300311, the first and second hybrid generations were obtained. They, together with the parental forms, were grown under autumn and spring sowing (winter crop and spring crop respectively, a total of four experimental variants). The seasonal experience option is labelled as E: E_1 as winter crop, E_2 as spring crop.

Conditions of the experiments

The research was carried out on the black soil field of the Plant Production Institute named after V.Ya. Yuryev of

the National Academy of Agrarian Sciences of Ukraine. Parental forms were sown in 2018, 2019 and 2020 in autumn and winter sown. Generations P_1, P_2, F_1, F_2 were grown in 2021 in winter and spring crops. The vegetation period of autumn sown plants was from October 2020 to July 2021; spring sown plants were grown since March 2021 to July 2021.

Figure 1. *a* — UA0300311, *b* — UA0300282 in winter crop; *c* — UA0300311, *d* — UA0300282 in spring crop.

Plot placement followed the scheme: P_1, P_2, $F_{1\ direct}$, $F_{2\ direct}$, P_1, P_2, $F_{1\ reverse}$, $F_{2\ reverse}$, P_1, P_2. Generations P1, P2, F1 were grown in plots consisting of 7 parallel rows, F2 was grown in plots of 10 parallel rows. Row length was 1 m and row spacing was 15 cm wide. Thirty kernels were sown in each row. 20 plants each were analyzed in P_1, P_2, F_1; at least 150 plants were analyzed in F_2. Weather conditions in all years were sufficient for the growth and development of einkorn.

Tillering counting

The total productive tillering on each plant was counted at the end of the growing season according to the methodological guidelines "Descriptors and data standard for wheat" (Li and Li, 2006).

Statistical analysis

Verification of data distribution by the number of productive tillering was carried out by the Shapiro — Wilk method. Two-sided Student's *t* test for unrelated groups was used to compare group averages, and dispersions were compared using Fisher's *F* test. Statistical hypotheses were tested at the significance level of 0.01.

Genetic analysis

Segregation analysis was performed using R SEA v2.0 software developed by Wang et al. (2022). In each of the four variants of the genetic experiment, the inheritance models with the three lowest Akaike index (AIC) values were selected for testing. The genetic model with the lowest AIC value and the minimum number of statistically significant indicators was taken as the optimal model.

The inheritance models

The following were considered as models of inheritance: MG major gene model, MX mixed model of the major gene and polygene system, A additive effect, AD additive-dominance effect, ADI additive-dominance-epistatic effect, EA equal additive effect, EAD equal additive-dominance effect, MX2-ADI-AD means a mixed model of two major genes with additive-dominance-epistatic effect plus a system of polygenes with additive-dominance effect, 2MG-EAD assumes the presence of two major genes with equal additive-dominance effect, MX1-AD-ADI assumes the presence of one major gene with additive-dominance effect and a series of polygenes, MX2-ADI-ADI assumes the presence of two major genes and a series of polygenes, 1MG-A assumes the presence of one major gene with additive effect, 2MG-EAD assumes the presence of two major genes with equal additive-dominance effect, MX2-EA-AD assumes the presence of two major genes with equal additive effect with a series of polygenes, 1MG-AD assumes acting of one major gene with additive-dominance effect, MX2-ADI-AD assumes acting of two major genes with additive-dominance-epistatic effect and a series of polygenes, 1MG-EAD assumes the presence of one major gene with equal additive-dominance effect, 2MG-A assumes the presence of two major genes with additive effect and 2MG-EA assumes the presence of two major genes with equal additive effect.

For testing the suitability of the selected candidate models, it was used the indicators: *U1 2 ,U22 , U32,* Uniformity test*; nW2,* Smirnov's test*; Dn* — Kolmogorov's test.

The genetic model with the lowest AIC value and the minimum number of statistically significant indicators (Akaike, 1977) is taken as the optimal one.

RESULTS AND DISCUSSION

Tillering of different einkorn accessions

The average plant tillering depended on vegetation conditions. At autumn sowing, the accession UA0300311 had an average productive tillering of 9.6 per plant, the accession UA0300282 had productive tillering 6.3 per plant. Cultivation at spring sowing increased the average productive tillering per plant: 14.1 and 7.2, respectively (Table 1). The accession UA0300311 is labelled as high tillering, UA0300282 — as low tillering. Phenotypes of F_1 hybrids in reciprocal crosses (Table 1) indicate the

dependence of tillering degree on the crossing direction; it may indicate the role of cytoplasmic heredity in formation of this trait. The standard deviation of plant tillering in the second hybrid generation exceeds these values in the parental forms and F_1 hybrids which provides material for selection for tillering degree.

We attribute the 32% increase in tillering of the accession UA0300311 in spring sowing (E2) compared to autumn sowing (E1) to its sensitivity to day length. When day lengthening in the first half of vegetation up to (19) hours on 22 June, plants of this accession delay their development in the tillering phase, which leads to the formation of additional fruit-bearing shoots, and the transition to earing is postponed to a later date. In fact, it behaves as a intermediate (winter-spring).

Two systems interact in determining the growth habit in wheat: the need for low temperatures during early developmental phases, commonly referred to as the need for vernalisation (controlled by *Vrn* genes), and the response to photoperiod (controlled by *Ppd* genes) (Xiao and He, 2020; Zhmurko, 2020). The accession UA0300311 does not exhibit the low temperature requirement characteristic of true winter plants, and the developmental delay in spring sowing is entirely determined by the gene controlling the photoperiod response. The second parental form - UA0300282 practically does not respond to the day lengthening factor.

Table 1. Statistical evaluation of plant tillering in generations of einkorn wheat hybrids

E	Generation	*n*	*Min*	*Max*	$\bar{x}$	*s*	*As*	*Ex*
Winter crop	P_1(UA0300311)	20	6.00	14.00	9.60	2.46	0.63	–0.16
	P_2(UA0300282)	20	3.00	11.00	6.30	2.36	0.63	0.31
	$F_1(P_1 \times P_2)$	20	3.00	12.00	6.50	2.76	0.97	0.44
	$F_2(P_1 \times P_2)$	176	2.00	30.00	7.74	4.14	1.85	1.29
	$F_1 (P_2 \times P_1)$	20	3.00	15.00	7.50	3.84	0.85	0.03
	$F_2 (P_2 \times P_1)$	155	2.00	40.00	9.74	5.64	2.42	0.20
Spring crop	P_1(UA0300311)	20	10.00	18.00	14.10	2.47	0.02	–0.59
	P_2(UA0300282)	20	5.00	11.00	7.20	1.99	0.72	–0.39
	$F_1(P_1 \times P_2)$	20	7.00	16.00	10.80	2.74	0.63	0.00
	$F_2(P_1 \times P_2)$	150	1.00	31.00	15.96	6.76	0.05	–0.35
	$F_1 (P_2 \times P_1)$	20	8.00	16.00	10.50	2.80	0.95	0.02
	$F_2 (P_2 \times P_1)$	166	4.00	33.00	15.07	6.52	0.77	0.36

Remarks: E, seasonal experience option; P_1 и P_2, parental accessions; F_1 и F_2, first and second generation hybrids, respectively; *n*, number of accession plants analysed; *Min*, minimum value; *Max*, maximum value; $\bar{x}$, arithmetic mean value; *s*, standard deviation; *As*, asymmetry index; *Ex*, excess ratio.

Models of tillering inheritance

The segregation for tillering in the F_2 hybrid generation depended on the crossing direction and growing conditions. The used program offered 24 inheritance models to describe the results of each genetic experiment. In order to select the most suitable ones, three candidate models were selected for testing in each of the four genetic experiments. The selection criterion was the lowest three AIC values (Table 2).

Table 2. Maximum likelihood values (MLV) and Akaike information criterion (AIC)

E	Crossing	Model	MLV	AIC
Winter crop	UA0300311 × UA0300282	2MG-EAD	–529.81	1067.62
		MX1-AD-ADI	–529.96	1069.92
		MX2-ADI-ADI	–539.65	1070.31
	UA0300282 × UA0300311	1MG-AD	–483.38	978.75
		2MG-EAD	–483.05	974.09
		MX2-ADI-AD	–482.49	972.97
Spring crop	UA0300311 × UA0300282	1MG-A	–228.71	467.43
		2MG-EAD	–228.60	465.20
		MX2-EA-AD	–232.01	455.63
	UA0300282 × UA0300311	1MG-EAD	–330.90	671.81
		2MG-A	–331.06	672.11
		2MG-EA	–328.51	665.02

Remarks: E, seasonal experience option; MG, major gene model; MX, mixed model of the major gene and polygene system; A, additive effect; AD, additive-dominance effect; ADI, additive-dominance-epistatic effect; EA, equal additive effect; EAD, equal additive-dominance effect; MX2-ADI-AD means a mixed model of two major genes with additive-dominance-epistatic effect plus a system of polygenes with additive-dominance effect.

In autumn sowing, the crossing result in the combination UA0300311×UA0300282of can be explained by such models. One of them 2MG-EAD assumes the presence of two major genes with equal additive-dominance effect. Another model MX1-AD-ADI assumes the presence of one major gene with additive-dominance effect and a series of polygenes. The third model MX2-ADI-ADI involves two major genes and a series of polygenes.

For the plants obtained at spring sowing, these are model 1MG-A (one major gene with additive effect), model 2MG-EAD (two major genes with equal additive-dominance effect) and model MX2-EA-AD (two major genes with equal additive effect with a series of polygenes).

In the reverse combination (UA0300282×UA0300311), the results obtained for the plants of autumn sowing is explained by the 1MG-AD model which assumes acting of one major gene with additive-dominance effect. This result is explained also by the 2MG-EAD model, according to which there are two major genes with equal additive-dominance effect, as well as by the MX2-ADI-AD model with two major genes with additive-dominance-epistatic effect and a series of polygenes.

In spring crop, the crossing results may be explained by the models 1MG-EAD (one major gene with equal additive-dominance effect), 2MG-A (two major genes with additive effect) and 2MG-EA (two major genes with equal additive effect).

Testing of genetic models

We tested suitability of the selected candidate models according to the indicators U_1^2, U_2^2, U_3^2, ${}_nW^2$ and D_n, the results of which are presented in Table 3. The genetic model with the lowest AIC value and the minimum number of statistically significant indicators (Akaike, 1977) is taken as the optimal one. The results are presented in Table 3. It is concluded that for plants derived from autumn sowing of UA0300311×UA0300282 combination, the most appropriate model that describes the mode of tillering inheritance is 2MG-EAD which assumes the presence of two major genes with equal additive-dominance effect.

In the plants from spring sowing, the segregation for tillering is described by the MX2-EA-AD model which assumes two major genes with equal additive effect, but presence of polygenes with additive-dominance effect is also appropriate. In the reverse combination (UA0300282×UA0300311), the optimal model that best describes the variance of tillering at autumn sowing is MX2-ADI-AD which assumes acting of two major genes with additive-dominance-epistatic effect as well as polygenes with additive-dominance effect.

The segregation for tillering at spring sowing is well described by the 2MG-EA model with two major genes with equal additive effect.

Parameters of the optimal genetic model for tillering trait

Table 4 presents the first and second order parameters of the optimal genetic model for the tillering trait. The genes are phenotypically different depending on sowing dates and crossing direction.

In the cross UA0300311×UA0300282, in plants from winter crop, the additive effect of the first pair of major genes is positive and equals 0.83. In plants from spring sowing, the additive effect of the first pair of major genes is also positive and is of 7.21. The additive effect of polygenes is of – 10.97, the dominant effect of polygenes is of 0.64.

In the reverse combination (UA0300282×UA0300311) at winter sowing, additive effect of the first pair of major genes is greater than that of the second pair of major genes in absolute value, respectively –16.06 and –13.62; the dominant effect of the first pair of major genes is much less than that of the second pair, respectively 0.56 and 5.01. The additive effect of polygenes is more strongly represented than the dominant one, respectively 28.03 and 0.74. The σ^2_{mg} and h^2_{mg}, due to the major gene, were 26.66 and 83.78, respectively. The genetic variance σ^2_{pg} and the inheritance of h^2_{pg} due to the polygene are zero. Consequently, the inheritance model does not assume the participation of the polygene.

At spring sowing, the additive effect of the main gene is negative and characterized by the value –2.00. In the plant group from autumn sowing, the heritability of the main gene in the combination UA0300311×UA0300282 is 68 %; at spring sowing, the heritability of the main gene is 71 % and the polygenic system accounts for 16 %. In the plant group of the reverse combination UA0300282×UA0300311 obtained from autumn sowing, the heritability determined by the main gene is 84 %; in the plants from spring sowing, the heritability of the main gene is of 92 % (Table 4).

Xie et al. (2006), observed that in bread wheat H461, low tillering was determined by two major nuclear genes with a series of polygenes one of which was a suppressor gene and had no reciprocal action. Du et al. (2011), for F_2 hybrids from a cross between bread wheat cultivars Mazhamai and Quality, showed that effective tillering was controlled by a pair of major genes and polygenes with the heritability of major genes being 0.56. Zhang et al. (2008), found that vigorous tillering is regulated by two pairs of major genes, one of which suppresses tillering.

In this study, it was found that the tillering trait in einkorn wheat shows a reciprocal effect in contrast to bread wheat. As well as in bread wheat, tillering is under the control of a small number of major genes with a system of polygenes that increase phenotypic diversity.

Table 3. Test for plant tillering inheritance genetic models suitability

E	Crossing	Model	Generation	$U_1^2(p)$	$U_2^2(p)$	$U_3^2(p)$	${}_nW^2(p)$	$D_n(p)$
E_1	UA0300311 × UA0300282	2MG-EAD	P_1 (UA0300311)	0.05(0.81)	0.04(0.85)	0.02(0.89)	0.07(0.77)	0.20(0.74)
			P_2 (UA0300282)	0.03(0.03*)	0.02(0.90)	0.02(0.89)	0.06(0.84)	0.22(0.65)
			F_1 ($P_1 \times P_2$)	0.10(0.75)	0.09(0.12)	0.001(0.99)	0.09(0.65)	0.28(0.36)
			F_2 ($P_1 \times P_2$)	0.01(0.90)	0.03(0.87)	0.03(0.033)	0.18(0.30)	0.08(0.19)
		MX1-AD-ADI	P_1 (UA0300311)	0.05(0.02*)	0.04(0.85)	0.02(0.89)	0.07(0.77)	0.20(0.74)
			P_2 (UA0300282)	0.03(0.87)	0.03(0.87)	0.001(0.97)	0.05(0.02*)	0.21(0.69)
			F_1 ($P_1 \times P_2$)	0.16(0.69)	0.07(0.79)	0.20(0.65)	0.10(0.60)	0.29(0.33)
			F_2 ($P_1 \times P_2$)	0.17(0.68)	0.25(0.62)	0.18(0.67)	0.20(0.28)	0.09(0.09)
		MX2-ADI-ADI	P_1 (UA0300311)	0.05(0.83)	0.04(0.83)	0.001(0.98)	0.07(0.78)	0.20(0.76)
			P_2 (UA0300282)	0.34(0.23)	0.88(0.59)	0.85(0.02*)	0.05(0.86)	0.21(0.72)
			F_1 ($P_1 \times P_2$)	0.14(0.70)	0.08(0.04*)	0.11(0.74)	0.10(0.61)	0.28(0.34)
			F_2 ($P_1 \times P_2$)	0.71(0.09)	0.76(0.54)	0.83(0.25)	0.19(0.11)	0.11(0.03*)
E_1	UA0300282 × UA0300311	1MG-AD	P_1(UA0300311)	0.93(0.04*)	0.82(0.04)	0.85(0.02)	0.89(0.07)	0.20(0.74)
			P_2(UA0300282)	0.03(0.87)	0.02(0.90)	0.02(0.89)	0.06(0.84)	0.22(0.65)
			F_1 ($P_2 \times P_1$)	0.07(0.79)	0.05(0.03*)	0.04(0.84)	0.05(0.85)	0.16(0.93)
			F_2 ($P_2 \times P_1$)	0.001(0.90)	0.01(0.91)	0.13(0.02*)	0.12(0.49)	0.08(0.03*)
		2MG-EAD	P_1 (UA0300311)	0.05(0.82)	0.04(0.85)	0.02(0.89)	0.07(0.77)	0.20(0.74)
			P_2 (UA0300282)	0.03(0.87)	0.02(0.90)	0.02(0.90)	0.06(0.84)	0.22(0.65)
			F_1 ($P_2 \times P_1$)	0.65(0.07)	0.79(0.04*)	0.83(0.03*)	0.84(0.02*)	0.85(0.16)
			F_2 ($P_2 \times P_1$)	0.001(0.95)	0.01(0.93)	0.01(0.91)	0.13(0.48)	0.07(0.03*)
		MX2-ADI-AD	P_1 (UA0300311)	0.30(0.58)	0.0001(0.98)	4.91(0.13)	0.15(0.37)	0.25(0.51)
			P_2 (UA0300282)	0.03(0.87)	0.03(0.89)	0.01(0.94)	0.06(0.84)	0.22(0.66)
			F_1 ($P_2 \times P_1$)	0.06(0.81)	0.03(0.86)	0.06(0.81)	0.07(0.76)	0.20(0.02*)
			F_2 ($P_2 \times P_1$)	0.73(0.04*)	0.085(0.07)	0.79(0.12)	0.73(0.14)	0.14(0.42)
E_2	UA0300311 × UA0300282	1MG-A	P_1 (UA0300311)	0.001(0.98)	0.0001(0.95)	0.10(0.75)	0.02(0.99)	0.12(1.00)
			P_2 (UA0300282)	0.05(0.82)	0.01(0.91)	0.17(0.68)	0.07(0.74)	0.24(0.55)
			F_1 ($P_1 \times P_2$)	0.04(0.84)	0.03(0.87)	0.02(0.89)	0.05(0.86)	0.22(0.64)
			F_2 ($P_1 \times P_2$)	0.01(0.94)	0.01(0.94)	0.0001(0.97)	0.03(0.96)	0.09(0.77)
		2MG-EAD	P_1 (UA0300311)	0.0001(0.98)	0.001(0.94)	0.10(0.71)	0.002(0.99)	0.12(0.98)
			P_2 (UA0300282)	0.02(0.88)	0.07(0.79)	0.22(0.64)	0.06(0.80)	0.20(0.75)
			F_1 ($P_1 \times P_2$)	0.06(0.80)	0.01(0.94)	0.41(0.52)	0.06(0.79)	0.24(0.56)
			F_2 ($P_1 \times P_2$)	0.001(0.94)	0.0001(1.00)	0.06(0.81)	0.05(0.86)	0.11(0.58)
		MX2-EA-AD	P_1 (UA0300311)	0.40(0.52)	0.28(0.59)	0.11(0.74)	0.06(0.80)	0.20(0.76)
			P_2 (UA0300282)	0.67(0.41)	0.78(0.38)	0.13(0.72)	0.13(0.46)	0.26(0.44)
			F_1 ($P_1 \times P_2$)	1.89(0.17)	1.09(0.30)	1.33(0.25)	0.26(0.18)	0.37(0.10)
			F_2 ($P_1 \times P_2$)	0.72(0.40)	0.45(0.50)	0.36(0.55)	0.12(0.52)	0.12(0.43)
E_2	UA0300282 × UA0300311	1MG-EAD	P_1 (UA0300311)	0.001(0.98)	0.001 (0.05*)	0.10(0.75)	0.02(0.99)	0.12(1.00)
			P_2 (UA0300282)	0.05(0.82)	0.01(0.91)	0.17(0.68)	0.07(0.04*)	0.24(0.55)
			F_1 ($P_2 \times P_1$)	0.09(0.76)	0.06(0.81)	0.05(0.82)	0.09(0.66)	0.23(0.61)
			F_2 ($P_2 \times P_1$)	0.001(0.99)	0.0001(0.98)	0.001(0.98)	0.05(0.86)	0.06(0.87)
		2MG-A	P_1 (UA0300311)	0.001(0.97)	0.08(0.78)	1.56(0.21)	0.05(0.86)	0.17(0.90)
			P_2 (UA0300282)	0.05(0.82)	0.01(0.01*)	0.17(0.68)	0.07(0.04*)	0.24(0.55)
			F_1 ($P_2 \times P_1$)	0.28(0.60)	0.01(0.94)	3.07(0.08)	0.15(0.39)	0.31(0.25)
			F_2 ($P_2 \times P_1$)	0.01(0.94)	0.0001(0.99)	0.04(0.83)	0.04(0.90)	0.08(0.62)
		2MG-EA	P_1 (UA0300311)	0.001(0.98)	0.001(0.95)	0.10(0.75)	0.02(0.99)	0.12(1.00)
			P_2 (UA0300282)	0.05(0.82)	0.01(0.01*)	0.17(0.68)	0.07(0.74)	0.24(0.55)
			F_1 ($P_2 \times P_1$)	0.09(0.76)	0.06(0.81)	0.05(0.82)	0.09(0.66)	0.23(0.61)
			F_2 ($P_2 \times P_1$)	0.0001(0.95)	0.01(0.93)	0.01(0.91)	0.04(0.92)	0.07(0.78)

Remarks: E, seasonal experience option; E_1, winter crop; E_2, spring crop; U_1^2, U_2^2, U_3^2, Uniformity test; ${}_nW^2$, Smirnov's test; D_n — Kolmogorov's test; p, significance level; *, $p < 0.01$.

Table 4. Parameters of 1st and 2nd tillering orders in optimal genetic models

E	Crossing	Model	1st order parameters						2nd order parameters			
			da	*db*	*ha*	*hb*	[*d*]	[*h*]	σ^2_{mg}	h^2_{mg} (%)	σ^2_{pg}	h^2_{pg}(%)
E_1	I	2MG-EAD	0.83	—	—	—	—	—	11.70	68.27	—	—
E_2		MX2-EA-AD	7.21	—	—	—	–10.97	0.64	32.60	71.27	7.39	16.05
E_1	II	MX2-ADI-AD	–16.06	–13.62	0.56	5.01	28.03	0.74	26.66	83.78	0.00	0.00
E_2		2MG-EA	–2.00	—	—	—	—	—	38.95	91.63	—	—

Remarks: E, seasonal experience option; E_1, winter crop; E_2, spring crop; I, UA0300311 × UA0300282; II, UA0300282 × UA0300311; da, additive effect of the first pair of major genes; db, additive effect of the second pair of major genes; [d], additive effect of polygene; [h], dominance effect of polygene; h, dominance effect of major gene; ha, dominance effect of the first pair of major genes; hb, dominance effect of the second pair of major genes; σ^2_{mg}, genetic variance for the major gene; h^2_{mg}, heritability of a trait determined by a major gene; σ^2_{pg}, genetic variance for the polygene; h^2_{pg}, heritability determined by polygene; «—», no value.

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