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INHERITANCE OF PLANT HEIGHT IN EINKORN WHEAT BY RESULTS OF SEGREGATION ANALYSIS

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ABSTRACT

The genetic control of plant height – important trait associated with yield – is practically not studied in diploid wheats. In this paper, using reciprocal crosses between two *Triticum monococcum* accessions – var. *monococcum* (UA0300311) and var. *nigricultum* (UA0300282) in autumn and spring sowing, inheritance of the plant height is studied. The sowing period significantly affects the expression of einkorn plant height. Data from the generations P_1, P_2, F_1, F_2 were used for segregation analysis. For a combination of UA0300311 × UA0300282, the optimal models for plant height inheritance are: at autumn sowing – one main gene with a negative complete dominant effect, its additive effect is –8.05; at spring sowing – one main gene with an additive-dominant effect, its additive effect is –24.51. For the reciprocal combination UA0300282 × UA0300311, at autumn sowing, the optimal model of plant height was one main gene with an equal additive-dominant effect, it additive effect is 10.94; at spring sowing – one main gene with a negative complete dominant effect, its additive effect is –18.37. The heritability was in all cases from 96.52% to 99.70%. The high dispersion of the trait in the second hybrid generation suggests that the studied parental forms differ not only in the main gene, as follows from the results of segregation analysis, but also in the system of modifier genes with a weak effect.

Keywords: Einkorn wheat, plant height, segregation analysis

INTRODUCTION

Plant height is an important characteristic related to both potential and actual yields, and one of the most informative predictive indicators. In wheat, this trait is inversely related to the coefficient of economic efficiency, which is the ratio of grain weight to vegetative weight. In spring bread wheat, a strong, year-independent, direct relationship between yield and plant height was observed (Volkova, 2016). The same pattern has been observed in winter bread wheat, and the range of height in which the maximum yield is formed has been identified (Samofalov et al., 2020; Zakharova et al., 2020). A plant height is also considered as one of the indicators of plant ecological plasticity in various soil and climatic conditions (Ripberger et al., 2015).

The disadvantage of tall plants is their tendency to lodging, which reduces real yield. The problem of lodging was solved by the creation of short-stemmed varieties, which led to the “green revolution”, which reduced the threat of famine (Sukhikh et al., 2021).

According to Zakharova et al. (Zakharova et al., 2020), the heritability of plant height is 65.2%, the share of gene-environment component accounts for 30.4% of phenotypic diversity, the environmental one – 0.9%.

In tetra- and hexaploid wheats have already registered 25 genes (*Rht1*–*Rht25*) that determine plant height (Mo et al., 2018). In the subgenome *A* derived from einkorn wheats, the genes are localized: *Rht7 (2AS)* (Yan and Zhang 2017; Divashuk et al. 2012), *Rht12 (5AL)* (Yan and Zhang, 2017; Rebetzke et al., 2012), *Rht18 (6A)* (Yan and Zhang, 2017; Yang et al., 2007), *Rht22 (7AS)* (Peng et al., 2011), *Rht24 (6AL)* (Tian et al., 2017), *Rht25 (6AS)* (Mo et al., 2018). Many of these genes are used in breeding programs on hexaploid (Tian et al., 2017; Cui et al., 2022) and tetraploid wheats (Duan et al., 2020).

Attention to the cultivated einkorn *Triticum monococcum* L. as a source of healthy food has grown substantially in recent decades. This explains the interest in studying the traits associated with yield, including the plant height.

Cultivated varieties of einkorn are prone to lodging, and reducing their height can weaken this disadvantage. For this purpose, agricultural techniques are used. So, at autumn sowing in comparison with spring sowing, higher plants are formed with increased potential yields, however also more prone to lodging. Taking into account the fact that this crop is adapted to harsh conditions, it is proposed to grow it at spring sowing, when low-growing, less lodging plants are formed (Ozturk et al., 2021).

It is also possible to reduce the plant height by breeding (Kefi et al., 2021). The material for this is the wide genetic diversity in plant height of both cultivated and wild einkorns (Karagoz and Zencirci, 2005; Seifolahpour et al., 2017).

For successful breeding, information about the inheritance type of this quantitative trait is necessary. For genetic study of quantitative traits in plants, Gai et al. (2003) developed the method "Mixed major genes plus polygenes inheritance analysis", that is the method of segregation analysis. Using it, you can determine the number of main genes and polygenes that control the trait. The method has been tested on a number of species. It's mogar (*Setaria italica* (L.) P.Beauv.) (Guo et al., 2021), ricinus (*Ricinus communis* L.) (Cui et al., 2019), buckwheat (*Fagopyrum esculentum* Moench) (Li et al., 2018), bread wheat (*Triticum aestivum* L.) (Xie et al., 2020) , durum wheat (*Triticum durum* Desf.) (Zhong et al., 2020; Gong et al., 2021), maize (*Zea mays* L.) (Wu et al., 2022).

Information on the inheritance of plant height of einkorn wheat is practically absent. So the purpose of this study was to perform segregation analysis of this trait in the species *Triticum monococcum* L. in winter and spring crops.

MATERIALS AND METHODS

Materials

In reciprocal crosses were used the accessions of *Triticum monococcum* L. from the National Bank of Plant Genetic Resources of Ukraine: UA0300311 var. *monococcum* originating from Syria and UA0300282 var. *nigricultum*, Hungary. The accession UA0300282 has a winter growth habit (heading at a short day), the average plant height according to four years of study is 135 cm, the ear is black. The accession UA0300311 is spring, plant height of 144 cm, light pink ear.

Conditions for conducting experiments

The studies were carried out on the experimental field of the Plant Production Institute named after V. Ya. Yuryev of the National Academy of Agrarian Sciences of Ukraine (chernozem of the eastern forest-steppe of Ukraine). The preceding crop was "black" fallow. Chemical fertilizers and plant protection substances were not used, the weeds were removed manually several times a season. Weather conditions in the research years are presented in Table 1. In the autumn-winter period, the temperature was above the long-term average, with the exception of November 2018. The amount of precipitation in October-November 2018 and November 2019 was less than the long-term average, and in 2020 close to it. In all years, the conditions were sufficient for successful overwintering of einkorn wheat plants during autumn sowing.

Table 1. Weather conditions during the research years

Indicator	Month										AT, °C TP, mm in E_1	AT, °C TP, mm in E_2
	10	11	12	1	2	3	4	5	6	7		
2018 year			2019 year									
AT, °C	+10.4	–0.7	–3.2	–5.2	–1.2	+3.7	+10.6	+17.6	+23.7	+20.8	+7.65	+15.28
TP, mm	20.3	20.5	73.3	57.6	8.7	16.2	39.5	68.8	18.1	64	387.0	206.6
2019 year			2020 year									
AT, °C	+10.6	+3.5	+1.6	–0.1	+0.3	+6.5	+8.8	+13.6	+22.1	+22.8	+8.97	+14.76
TP, mm	72.3	19.7	27.7	29.9	67.2	17.7	21.8	137.9	68.4	106.7	569.3	352.5
2020 year			2021 year									
AT, °C	+12.4	+2.6	–3.1	–2.5	–5.0	+1.1	+8.3	+15.7	+20.5	+24.7	+7.47	+14.06
TP, mm	40.5	40.7	24.6	70.4	59.8	18.2	41.7	52.7	68.4	7.3	424.3	188.3
Average perennial												
AT, °C	+7.7	+1.3	–3.5	–6.0	–5.3	0.0	+8.9	+15.4	+19.2	+21.2	+5.89	+12.94
TP, mm	38.1	39.4	38.0	38.7	31.4	28.8	32.3	45.5	52.9	59.1	404.2	218.6

Note: E_1, autumn sowing; E_2, spring sowing; AT, average temperature; TP, total precipitation; mm, millimeters; °C, degrees Celsius.

The resumption of vegetation, as well as spring sowing in the research years took place at a slightly higher temperature and less amount of precipitation compared to long-term data, however, the development of plants was provided with sufficient reserves of winter moisture.

The critical periods of formation and development of generative organs for the plants of autumn sowing fall in May, for the plants of spring sowing – in June. In our study, this period coincided with favourable conditions for both temperature and moisture, except for the dry June 2019. The formation of plant height in the plants of autumn sowing in June also occurred under favorable conditions, but in July 2021 in the plants from spring sowing under drought.

Staging crosses

The experiment was started on the autumn sowing of 2018. Hybrids of the first generation (F_1) in direct (di.)

crossing *T monococcum* var. *nigricultum* UA0300282 × *T. monococcum* var. *monococcum* UA0300311 and reciprocal (rec.) *T. monococcum* var. *monococcum* UA0300311 × *T monococcum* var. *nigricultum* UA0300282 were obtained in 2019, the seeds were used to obtain F_2. Repeatedly crosses to produce F_1 were carried out in 2020 in plots sown in autumn 2019. Parental forms (P_1, P_2) before the start of the experiment were studied for two years, in 2018 and 2019.

During the experiment, all four generations (P_1, P_2, F_1, F_2) were grown at two sowing times. Autumn sowing was carried out in October 2020, the growing season ended in July 2021. Spring sowing was carried out in March 2021, ripening came in July 2021.

Before the experiment, the grains were manually freed from hulls. The plots were placed according to the scheme: P_1, P_2, $F_{1di.}$, $F_{2di.}$, P_1, P_2, $F_{1rec.}$, $F_{2rec.}$, P_1, P_2. Sowing was carried out manually on tapes 1 m wide with a row spacing of 15 cm. Thirty grains were placed in each of the rows. Plant height was measured after plant maturity on the main stems, in plots P_1, P_2, $F_{1di.}$, $F_{1rec.}$ in 20 plants; in $F_{2di.}$, $F_{2rec.}$ at least in 180 plants. To avoid edge effects, non-edge plants were selected for height measurements, in accordance with the guidelines "Descriptors and data standard for wheat" (Li and Li, 2006).

Methods of data analysis

The degree of dominance (*Hp*) of plant height in F_1 hybrids was determined by the Griffing (1956) formula:

$$Hp = \frac{F_1 - M_p}{P_{\max} - M_p}$$

where F_1 is the arithmetic mean value of the trait in the hybrid of the first generation; M_p is the arithmetic mean of the parent forms; P_{max} is the higher parent form.

Segregation analysis was performed using the R SEA v2.0 software developed by Wang et al. (2022) under the guidance of Zhang Yuan-Ming. The maximum likelihood value (MLV) and akaike information criterion (AIC) of the genetic model are calculated. Three models were selected as candidates. The candidate model was tested using the uniformity, Smirnov and Kolmogorov tests.

The calculations were performed using the SPSS 25 software. Statistical hypotheses were tested at a significance level of 0.05 using two-sided Student's t-test for unrelated groups. The graphics were made using the GraphPad Prism 9 software.

RESULTS

Plant height in different generations

The average plant height of the parent forms at autumn sowing was 124 and 138 cm. The same forms at spring sowing were 20% lower (103 and 112 cm, Table 2, Figure 1). The plant height of the F_1 hybrids determined by the gene interaction in influencing the trait, which in turn is characterized by the of dominance degree (*Hp*), depended on the crossing direction what indicates the role of cytoplasmic heredity in the formation of this quantitative trait.

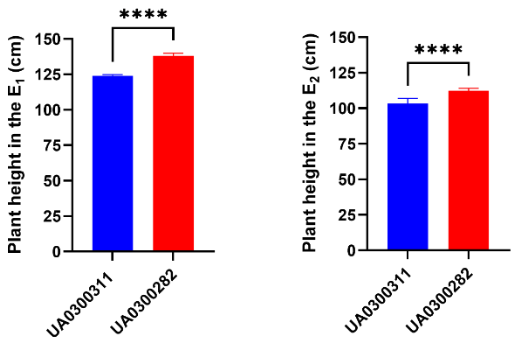

Figure 1. Plant height at different sowing times
Note: E_1, autumn sowing; E_2, spring sowing;****, $P < 0.0001$

Table 2. Statistical evaluation of plant height in different populations of einkorn wheat

E	Generation	*n*	*Min*	*Max*	$\bar{x}$	*Hp*	*s*	*As*	*Ex*
E_1	P_1(UA0300311)	20	122.8	125.3	124.1	—	0.75	–0.06	–0.53
	P_2(UA0300282)	20	135.5	141.5	137.9	—	2.05	0.46	–0.85
	$F_1(P_1 \times P_2)$	20	126.5	131.7	128.7	–0.33	1.67	0.43	–0.62
	$F_2(P_1 \times P_2)$	182	67.0	149.0	128.2	—	12.94	–2.68	9.34
	$F_1 (P_2 \times P_1)$	20	130.5	140.5	135.3	0.63	3.29	0.10	–0.02
	$F_2 (P_2 \times P_1)$	188	66.0	149.0	130.1	—	14.19	–2.71	8.14
E_2	P_1(UA0300311)	20	98.0	110.0	103.3	—	3.68	0.41	–0.27
	P_2(UA0300282)	20	110.0	115.5	112.4	—.	1.59	0.32	0.48
	$F_1(P_1 \times P_2)$	20	102.0	108.0	105.0	–0.62	2.09	–0.10	–1.48
	$F_2(P_1 \times P_2)$	180	40.0	127.0	88.9	—	20.97	–0.73	–0.39
	$F_1 (P_2 \times P_1)$	20	102.0	106.5	104.2	–0.80	1.47	0.19	–0.91
	$F_2 (P_2 \times P_1)$	186	38.0	119.0	90.6	—	18.69	–1.00	0.35

Note: E, sowing time; E_1, autumn sowing; E_2, spring sowing; P_1 and P_2, parent forms; F_1 and F_2, hybrids of the first and second generations respectively; *n*, sample number; *Min*, the minimum value; *Max*, the maximum value; $\bar{x}$, the arithmetic mean; *Hp*, degree of dominance; *s*, standard deviation; *As*, an asymmetry index; *Ex*, an excess rate; "—", no value.

In plants from direct crosses sown in autumn, *Hp* = –0.33, what corresponds to the weak dominance of the lower parent. In the reciprocal combination, value of the indicator was *Hp* = 0.63 which corresponded to the average degree of dominance of the taller parent. At spring sowing, the trait of the lower parental form dominated in both combinations, the dominance degree *Hp* is respectively –0.62 and –0.80.

Models of plant height inheritance

The choice of the optimal genetic model was based on AIC values obtained from plant height data in generations P_1, P_2, F_1 and F_2. The genetic model with the lowest AIC value and the lowest number of statistically significant indicators is taken as optimal (Akaike, 1977). This condition was met by three models that were selected for testing. In the combination of UA0300311 × UA0300282 during autumn sowing, the following models became candidates: 1MG-AD, 1MG-NCD, 2MG-EA. For plants obtained during spring sowing, these are the models 1MG-AD, 1MG-A and 2MG-EAD (Table 3). In the reciprocal combination (UA0300282 × UA0300311) for plants from autumn sowing, this condition is satisfied with the models 1MG-AD, 1MG-EAD and 2MG-EAD, with spring sowing — models 1MG-AD, 1MG-NCD and 2MG-EAD. The value of the maximum likelihood (MLV) function is also presented in Table. 3.

Table 3. Akaike information criterion (AIC) and Maximum likelihood values (MLV)

E	Crossing	Model	MLV	AIC
E_1	UA0300311 × UA0300282	1MG-AD	–590.69	1193.38
		1MG-NCD	–590.65	1191.30
		2MG-EA	–592.15	1192.30
	UA0300282 × UA0300311	1MG-AD	–611.92	1235.83
		1MG-EAD	–612.12	1234.25
		2MG-EAD	–617.14	1242.28
E_2	UA0300311 × UA0300282	1MG-AD	–345.67	703.33
		1MG-A	–348.07	706.14
		2MG-EAD	–346.82	705.63
	UA0300282 × UA0300311	1MG-AD	–471.91	955.81
		1MG-NCD	–472.68	955.36
		2MG-EAD	–473.89	955.78

Note: E, sowing time; E_1, autumn sowing; E_2, spring sowing; MLV, maximum likelihood value; AIC, the Akaike criterion; 1MG, one main gene; 2MG, the two main genes; A, additive effect; AD, additive-dominant effect; EA, equally additive effect; EAD, equally additive-dominant effect; NCD, negatively completely dominant effect.

Candidate models were tested for fitting, and according to the indicators U_1^2, U_2^2, U_3^2, ${}_nW^2$, D_n, the one whose AIC value is the lowest, as well as the lowest number of levels of statistical significance (Table 4) was chosen as optimal. UA0300311 × UA0300282, the most suitable inheritance model is 1MG-NCD, according to which, differences in the height of parental forms are due to one major gene with a negative overall dominant effect. In plants from spring snowing, the height distribution is described by the 1MG-AD model, which suggests the presence of one main gene with an additive-dominant effect.

Parameters of the optimal genetic model of the trait of plant height

The genes manifest different effect on a trait depending on the crossing direction and the environment created by the timing of sowing. In the cross UA0300311 × UA0300282, in the plants of autumn sowing, the additive effect of the main gene is negative and equals –8.05. In the plants from spring sowing, the additive effect of the main gene is also negative and manifests itself more strongly, amounting to –24.51. The dominant effect of the main gene is characterized as 11.56. The value $|h/d| < 1$, means that the genetic effect of the main gene is dominated by an additive component. In the reciprocal combination of UA0300282 × UA0300311 during autumn sowing, the additive effect of the main gene is positive, amounting to 10.94. In spring sowing, the additive effect of the main gene is negative and characterized as –18.37.

The heritability of plant height in the model of the main gene is practically independent of the sowing time. In the group of plants from autumn sowing, heritability in direct combination is 99.70%, in the plants of spring sowing, heritability is 97.23%. In the plants of the reciprocal combination obtained from autumn sowing, heritability is 98.12%, in plants from spring sowing, heritability is 96.52% (Table 5).

The distribution curves of the optimal genetic model of the plant height in reciprocal combinations at different sowing times are presented in Figure 2.

The high dispersion of the trait in the second hybrid generation suggests that the studied parental forms differ not only in the main gene, as follows from the results of segregation analysis, but also in the system of modifier genes with a weak effect.

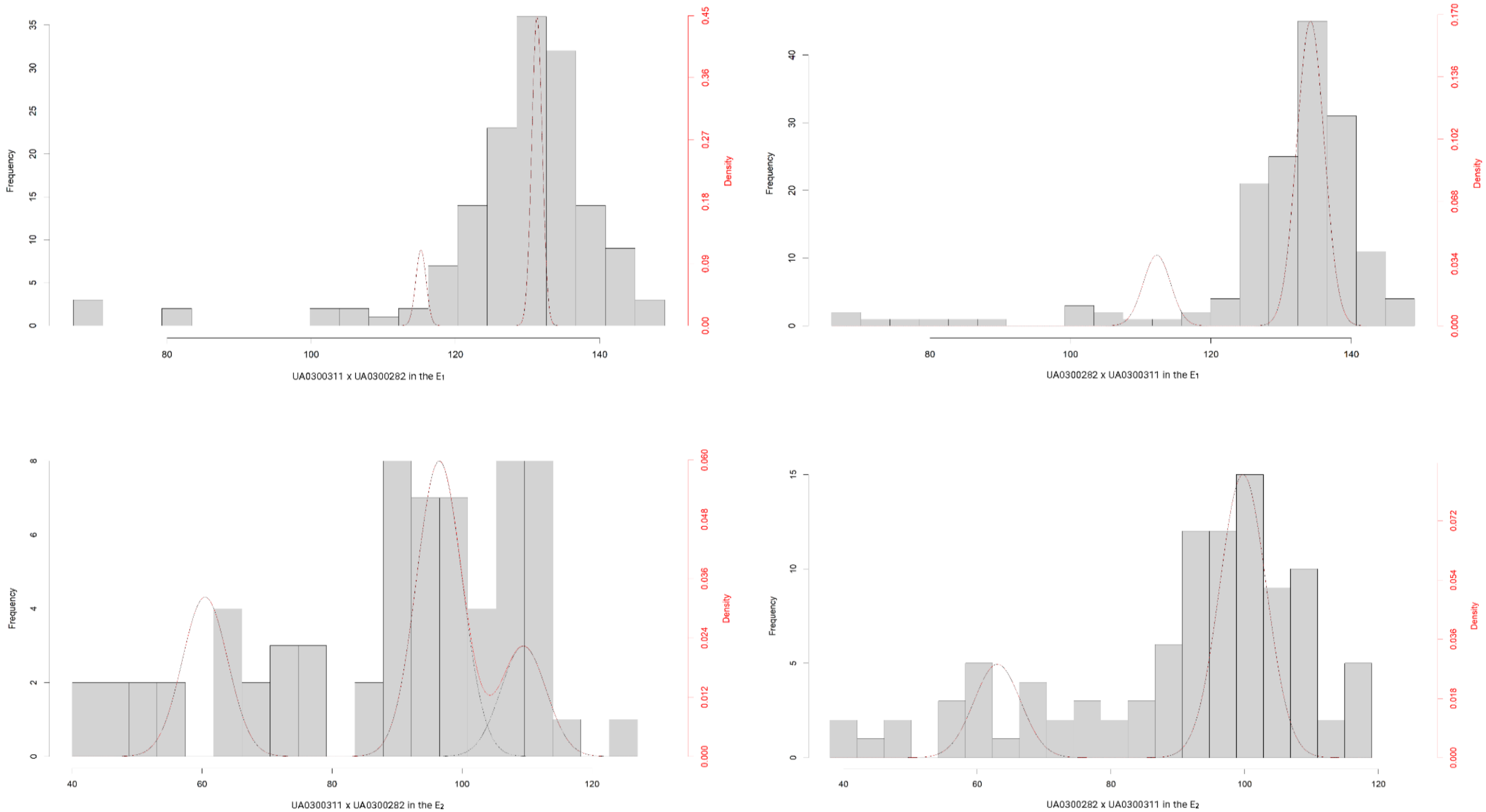

Figure 2. Distributions of optimal genetic models

Note: E_1, autumn sowing; E_2, spring sowing; columns, frequency; solid line and theoretical, mixed; dashed line, component.

Table 4. Test of fitness of selected genetic models of plant height inheritance

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	1MG-AD	P_1 (UA0300311)	0.00(0.98)	0.01(0.91)	0.12(0.72)	0.03(0.95)	0.14(0.96)
			P_2 (UA0300282)	0.02(0.88)	0.00(0.98)	0.24(0.62)	0.04(0.92)	0.19(0.79)
			F_1 ($P_1 \times P_2$)	0.01(0.89)	0.00(0.97)	0.16(0.68)	0.02(0.97)	0.15(0.94)
			F_2 ($P_1 \times P_2$)	0.03(0.85)	0.00(0.95)	0.22(0.63)	0.05(0.84)	0.05(0.66)
		1MG-NCD	P_1 (UA0300311)	0.00(0.98)	0.01(0.91)	0.12(0.72)	0.03(0.95)	0.14(0.96)
			P_2 (UA0300282)	0.02(0.88)	0.00(0.98)	0.24(0.62)	0.04(0.92)	0.19(0.79)
			F_1 ($P_1 \times P_2$)	0.01(0.89)	0.00(0.97)	0.16(0.68)	0.02(0.97)	0.15(0.94)
			F_2 ($P_1 \times P_2$)	0.03(0.85)	0.00(0.94)	0.19(0.65)	0.05(0.85)	0.05(0.66)
		2MG-EA	P_1 (UA0300311)	0.00(0.98)	0.01(0.91)	0.12(0.72)	0.03(0.95)	0.14(0.96)
			P_2 (UA0300282)	0.02(0.88)	0.00(0.98)	0.24(0.62)	0.04(0.92)	0.19(0.79)
			F_1 ($P_1 \times P_2$)	0.01(0.89)	0.00(0.97)	0.16(0.68)	0.02(0.97)	0.15(0.94)
			F_2 ($P_1 \times P_2$)	4.22(0.03*)	2.62(0.10)	2.16(0.14)	0.59(0.02*)	0.12(0.01*)
E_1	UA0300282 × UA0300311	1MG-AD	P_1(UA0300311)	0.02(0.88)	0.00(0.98)	0.24(0.62)	0.04(0.92)	0.19(0.79)
			P_2(UA0300282)	0.00(0.98)	0.01(0.91)	0.12(0.72)	0.03(0.95)	0.14(0.96)
			F_1 ($P_2 \times P_1$)	0.00(0.97)	0.00(0.94)	0.01(0.89)	0.10(0.55)	0.23(0.54)
			F_2 ($P_2 \times P_1$)	0.02(0.88)	0.00(0.93)	0.04(0.82)	0.07(0.73)	0.06(0.54)
		1MG-EAD	P_1 (UA0300311)	0.02(0.88)	0.00(0.98)	0.24(0.62)	0.04(0.92)	0.19(0.79)
			P_2 (UA0300282)	0.00(0.98)	0.01(0.91)	0.12(0.72)	0.03(0.95)	0.14(0.96)
			F_1 ($P_2 \times P_1$)	0.00(0.97)	0.00(0.94)	0.01(0.89)	0.10(0.55)	0.23(0.54)
			F_2 ($P_2 \times P_1$)	0.01(0.90)	0.00(0.95)	0.06(0.80)	0.06(0.76)	0.05(0.65)
		2MG-EAD	P_1 (UA0300311)	0.02(0.88)	0.00(0.98)	0.24(0.62)	0.04(0.92)	0.19(0.79)
			P_2 (UA0300282)	0.00(0.98)	0.01(0.91)	0.12(0.72)	0.03(0.95)	0.14(0.96)
			F_1 ($P_2 \times P_1$)	0.00(0.97)	0.00(0.94)	0.01(0.89)	0.10(0.55)	0.23(0.54)
			F_2 ($P_2 \times P_1$)	0.16(0.68)	0.00(0.93)	3.54(0.05)	0.21(0.23)	0.10(0.08)
E_2	UA0300311 × UA0300282	1MG-AD	P_1 (UA0300311)	0.01(0.90)	0.00(0.94)	0.04(0.82)	0.02(0.98)	0.12(0.98)
			P_2 (UA0300282)	0.00(0.95)	0.00(0.93)	0.00(0.93)	0.02(0.99)	0.13(0.97)
			F_1 ($P_1 \times P_2$)	0.00(0.96)	0.05(0.81)	0.54(0.45)	0.05(0.84)	0.19(0.78)
			F_2 ($P_1 \times P_2$)	0.00(0.92)	0.02(0.87)	0.08(0.77)	0.03(0.96)	0.06(0.90)
		1MG-A	P_1 (UA0300311)	0.01(0.90)	0.00(0.94)	0.04(0.82)	0.02(0.98)	0.12(0.98)
			P_2 (UA0300282)	0.00(0.95)	0.00(0.93)	0.00(0.93)	0.02(0.99)	0.13(0.97)
			F_1 ($P_1 \times P_2$)	0.00(0.96)	0.05(0.81)	0.54(0.45)	0.05(0.84)	0.19(0.78)
			F_2 ($P_1 \times P_2$)	0.01(0.89)	0.025(0.87)	0.01(0.90)	0.05(0.82)	0.06(0.89)
		2MG-EAD	P_1 (UA0300311)	0.01(0.90)	0.00(0.94)	0.04(0.82)	0.02(0.98)	0.12(0.98)
			P_2 (UA0300282)	0.00(0.95)	0.00(0.93)	0.00(0.93)	0.02(0.99)	0.13(0.97)
			F_1 ($P_1 \times P_2$)	0.00(0.96)	0.05(0.81)	0.54(0.45)	0.05(0.84)	0.19(0.78)
			F_2 ($P_1 \times P_2$)	0.00(0.99)	0.00(0.93)	0.08(0.77)	0.03(0.95)	0.05(0.96)
E_2	UA0300282 × UA0300311	1MG-AD	P_1 (UA0300311)	0.01(0.90)	0.00(0.94)	0.04(0.82)	0.02(0.98)	0.12(0.98)
			P_2 (UA0300282)	0.00(0.95)	0.00(0.93)	0.00(0.93)	0.02(0.99)	0.13(0.97)
			F_1 ($P_2 \times P_1$)	0.00(0.94)	0.00(0.96)	0.18(0.66)	0.03(0.97)	0.14(0.96)
			F_2 ($P_2 \times P_1$)	0.00(0.99)	0.00(0.99)	0.00(0.98)	0.01(1.00)	0.03(0.99)
		1MG-NCD	P_1 (UA0300311)	0.01(0.90)	0.00(0.94)	0.04(0.82)	0.02(0.98)	0.12(0.98)
			P_2 (UA0300282)	0.00(0.95)	0.00(0.93)	0.00(0.93)	0.02(0.99)	0.13(0.97)
			F_1 ($P_2 \times P_1$)	0.00(0.94)	0.00(0.96)	0.18(0.66)	0.03(0.97)	0.14(0.96)
			F_2 ($P_2 \times P_1$)	0.01(0.91)	0.02(0.88)	0.03(0.85)	0.02(0.99)	0.04(0.98)
		2MG-EAD	P_1 (UA0300311)	0.01(0.90)	0.00(0.94)	0.04(0.82)	0.02(0.98)	0.12(0.98)
			P_2 (UA0300282)	0.00(0.95)	0.00(0.93)	0.00(0.93)	0.02(0.99)	0.13(0.97)
			F_1 ($P_2 \times P_1$)	0.00(0.94)	0.00(0.96)	0.18(0.66)	0.03(0.97)	0.14(0.96)
			F_2 ($P_2 \times P_1$)	0.02(0.86)	0.02(0.88)	0.00(0.93)	0.04(0.92)	0.06(0.82)

Note: E, sowing time; E_1, autumn sowing; E_2, spring sowing; U_1^2, U_2^2, U_3^2, Uniformity test; ${}_nW^2$, Smirnov's test; D_n, Kolmogorov's test; P, level of significance; *, $P < 0.05$.

Table 5. Parameters of the 1st and 2nd order of plant height in optimal genetic models

E	Crossing	Model	1st order parameters		2nd order parameters	
			d	h	σ^2_{mg}	h^2_{mg}(%)
E_1	I	1MG-NCD	–8.05	—	167.05	99.70
E_2		1MG-AD	–24.51	11.56	427.56	97.23
E_1	II	1MG-EAD	10.94	—	197.51	98.12
E_2		1MG-NCD	–18.37	—	337.21	96.52

Note: E, sowing time; E_1, autumn sowing; E_2, spring sowing; I, UA0300311 × UA0300282; II, UA0300282 × UA0300311; d, the additive effect of the main gene; h, the dominant effect of the main gene; σ^2_{mg}, major gene variance; h^2_{mg}(%), heritability of major gene; "—", no value.

DISCUSSION

The plant height depends on the growing conditions. For example, water scarcity reduces the height of wheat plants (Wu et al., 2008; Ye et al., 2015). Ren et al. (2016) believe that the activity of genes responsible for plant height depends on the characteristics of the aquatic environment, and this is reflected in space-time models of gene expression at different stages of plant development (Zhang et al., 2012).

The sowing timing determines a complex of factors affecting the plant height. So, at spring sowing, in comparison with the autumn sowing, the growing season is reduced, all phases of plant development are shifted to a later date which is characterized by a higher temperature and moisture deficiency. It can explain the fact that plants from spring sowing in our experiments are lower than plants formed during autumn sowing. Also, against this intense background, the variation of plants increases in comparison with autumn sowing, which manifests itself, in particular, in a significant increase in the standard deviation in the more sensitive sample P1 (UA0300311) (Table 2).

Genetic control of the wheat plants height has been studied mainly on polyploid species. These experiments typically used short-stemmed forms with the genes inherited from the varieties Akakomughi or Norin 10, as well as mutants (Rht) (Kaya et al., 2015; Sukhikh et al., 2021). Genetic studies on polyploid wheat Halloran (1974) showed that plant height is under the control of two genes with a dominant effect. Chen (2011) concluded that this trait is controlled by a single not fully dominant gene. Yao et al. (2011) believe that the wheat plant height can be controlled by three-four pairs of major genes, and the constituents of this trait may be under the control of one to three pairs of major genes with an additive and wholly or partially dominant effect, with the main one being the additive effect. The presence of three pairs of genes that determine the wheat plant height is indicated by Xue et al. (2011). In the researches of Dagustu (2008), possible heterotic effects as well dominance for plant height was observed and it was concluded that both additive and non-additive gene actions are responsible for existence of variability on this trait. Istipliler et al. (2015), in hybrids between bread wheat cultivars carrying plant height reduced genes, observed negligible positive and negative effects of general combining ability and positive and significant effect of specific combining ability; low rations of wide as well as narrow sense heritabilities showed that nonadditive effects controlled the trait studied.

Chinese scientists have performed a number of genetic studies of the height of wheat plants using segregation analysis. Du et al. (2011) on the F_2 of hybrids from crossing of bread wheat varieties Mazhamai × Quality showed that plant height is controlled exclusively polygenically, without the main gene. Bi et al. (2013) on generations P_1, P_2, F_1, F_2 and F_3 from crossing varieties Xinong 817 × Chinese Spring concluded that the inheritance of wheat plant height was fitted by one major gene with additive effect plus additive-dominance polygenes model. Li et al. (2013) in experiments with the F_7 group obtained on recombinant inbred lines (RILs) from crossing Xiaoyan81 × Xinong1376, concluded that the plant height is controlled by two pairs of main genes with an additive-epistatic effect and polygenes, the heritability of this trait was 82%. Wen et al. (2018) on a group of F_2 hybrids from crossing Ningmai 9 × Zhenmai 168 showed that plant height is controlled by two main genes with an additive-dominant-epistatic effect, together with polygenes that exhibit an additive-dominant effect. The heritability of the plant height under control of the main gene under these conditions is 65%. Xie et al. (2020) based on the crossing of varieties Pingdong 34 and Barran, concluded that the plant height is determined by two pairs of main genes with a cumulative effect plus polygenes with an additive effect. The additive value of the first pair of the main genes controlling the plant height was 5.15, the heritability of plant height under the control of the main gene is 59%, and the heritability under polygenic control is 40%. Zhong et al. (2020), studying the hard wheat ANW16G, concluded that the plant height is controlled by two main genes with an additive-dominant-epistatic effect. With this control, the heritability of the plant height is 93%. Gong et al. (2021) in experiments on durum wheat ANW16F concluded that plant height is controlled by two main genes with an additive-dominant-epistatic effect, where the additive effect being predominant, the trait heritability being 86%.

As we can see, various genetic systems have been discovered, under the control of which the wheat plant height is located. Most authors conclude that there is a small number of genes (1-4 pairs) with a strong effect and a system of genes with a weak effect, the so-called modifier genes or polygenes, in the genetic control system of this trait.

The ambiguous results obtained by different authors using segregation analysis may be related to the genetic diversity of the source material. Another reason may be differences in growing conditions. Specific gene-environment interactions should also be pointed out, as well as different genetic experimentation schemes.

In our study on progeny from reciprocal crosses (direct UA0300311 × UA0300282, reciprocal UA0300282 × UA0300311) under different growing conditions (winter and spring crop), it was found that the plant height of einkorn wheat is controlled by one major gene with different degree of dominance as well as additive effect.

In conclusion, it should be noted that one of the most important agronomic traits of wheat, plant height, depends on both genetic and environmental factors, but the genetic factor is the determining factor (Lyu et al., 2021). The next step in this work could be the localization of QTLs using molecular markers.

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