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# INHERITANCE OF GROWTH HABIT IN EINKORN WHEAT

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***Aim.*** *Find out the inheritance patterns of the trait «winterness / springness» in hybrids between representatives of einkorn wheat species.* ***Methods.*** *Crossings were carried out using the «single cross» method. The nature of inheritance of the growth habit was determined using hybridological analysis.* ***Results.*** *It has been shown that in the hybrids of wild wheat forms T. boeoticum and T. urartu with cultivated T monococcum and T. sinskajae, the winter growth habit of wild forms dominates over the spring one of cultivated forms. Differences in «winterness / springness» phenotype between parental forms in crosses of T. monococcum var. macedonicum with T. urartu var. spontaneorubrum and T. boeoticum var. bicolor; T. sinskajae var. sinskajae with T. urartu var. spontaneorubrum and T. boeoticum var. thaoudar; T. boeoticum var. thaoudar with T. monococcum var. monococcum, T. sinskajae var. sinskajae and T.monococcum var. macedonicum; T. boeoticum var. kurbagalensense with T. sinskajae var. sinskajae and T.monococcum var. monococcum are controlled by a single gene. The difference between the two wild forms in crossing T. boeoticum var. thaoudar × T. boeoticum var. kurbagalensense is controlled by two genes. In the crosses T. boeoticum var. thaoudar with T. monococcum var. monococcum, T. sinskajae var. sinskajae and T. monococcum var. macedonicum; T. boeoticum var. kurbagalensense × T. sinskajae var. sinskajae, the parental forms also differ digenously.* ***Conclusions.*** *Winterness of einkorn wheat wild forms dominates over the springness of cultivated forms. The difference in the growth habit between the studied einkorn forms is due to differences in 1–2 pairs of genes.*

***Keywords:*** *einkorn wheat, growth habit, winterness, springness, inheritance.*

**Introduction.** A number of studies have proven the value of einkorn wheat for a healthy diet (Di Stasio et al., 2020; Picascia et al., 2020). This ancient crop is little affected by «industrial» breeding and therefore low productive. Increasing yield is the main task of its genetic improvement. An important factor in stable yields is adaptability to growing conditions, among which is growth habit which is determined by the need for low temperatures in early development phases, response to day length and development rate (Yang, 2012). Spring wheats go through the whole development cycle during one spring-summer season. Winter wheats are sown in the autumn, they remain in the vegetative phase during the winter and move on to generative development in following year. In intermedial («semi-winter») forms, generative shoots can be obtained both during autumn and spring sowing. Winter wheat has a longer period of accumulation of plastic substances than spring wheat as a result of which it is more productive.

To increase einkorn productivity in the southern latitudes, it is grown in a winter crop. In temperate latitudes, the risk factor is the non-resistance of spring forms to overwintering factors, and this necessitates creation of truly winter forms. In diploid and polyploid wheats, a number of genes have been identified that determine the growth habit: *Vrn1*, *Vrn2*, *Vrn3*, *Vrn4* (Muterko et al., 2015).

In order to carry out breeding work to create einkorn varieties with desired properties, it is necessary to expand the circle of involved initial forms with information about inheritance of the «winterness / springness» trait in them.

All of the above determined the purpose of the study: to find out how winterness and springness are inherited in a representatives of einkorn wheat species.

### Materials and methods

Seven einkorn accessions were used for the crosses, (table 1), with the participation of which 10 hybrids were obtained (table 2).

**Table 1. Einkorn wheat accessions used in the study**

| Variety | NNCU | OC | Abbreviation | GH | HD |
|---|---|---|---|---|---|
| *T. monococcum* var. *macedonicum* | UA0300113 | SYR | *T.mon*.v.*mac* | spring | 14.06 |
| *T. monococcum* var. *monococcum* | UA0300221 | AZE | *T.mon*.v.*mon* | spring | 18.06 |
| *T. sinskajae* var. *sinskajae* | UA0300224 | RUS | *T.sin*.v.*sin* | spring | 18.06 |
| *T. boeoticum* var. *thaoudar* | UA0300400 | ARM | *T.boe*.v.*tha* | int | 29.06* |
| *T. boeoticum* var. *kurbagalensense* | UA0300401 | UKR | *T.boe*.v.*kur* | winter | — |
| *T.boeoticum* var. *bicolor* | UA0300336 | LBN | *T.boe*.v.*bic* | winter | — |
| *T. urartu* var. *spontaneorubrum* | UA0300253 | ARM | *T.ura*.v.*spon* | winter | — |

Note: NNCU — Number of the National Catalog of Ukraine, OC — origin country, GH — Growth habit, HD — Heading date at spring sowing, int — intermediate («semi-winter»), * — headed single plants, «—» — the value is missing.

**Table 2. Hybrid combinations obtained in the experiment**

| Cross No. | Hybrid combinations | Abbreviation |
|---|---|---|
| 1 | *T. monococcum* var. *macedonicum* × *T. urartu* var. *spontaneorubrum* | *T.mon*.v.*mac* × *T.ura*.v.*spon* |
| 2 | *T. monococcum* var. *macedonicum* × *T. boeoticum* var. *bicolor* | *T.mon*.v.*mac* × *T.boe*.v.*bic* |
| 3 | *T. sinskajae* var. *sinskajae* × *T. urartu* var. *spontaneorubrum* | *T.sin*.v.*sin* × *T.ura*.v.*spon* |
| 4 | *T. sinskajae* var. *sinskajae* × *T. boeoticum* var. *thaoudar* | *T.sin*.v.*sin* × *T.boe*.v.*tha* |
| 5 | *T. boeoticum* var. *thaoudar* × *T. monococcum* var. *monococcum* | *T.boe*.v.*tha* × *T.mon*.v.*mon* |
| 6 | *T. boeoticum* var. *thaoudar* × *T. sinskajae* var. *sinskajae* | *T.boe*.v.*tha* × *T.sin*.v.*sin* |
| 7 | *T. boeoticum* var. *thaoudar* × *T. boeoticum* var. *kurbagalensense* | *T.boe*.v.*tha* × *T.boe*.v.*kur* |
| 8 | *T. boeoticum* var. *thaoudar* × *T. monococcum* var. *macedonicum* | *T.boe*.v.*tha* × *T.mon*.v.*mac* |
| 9 | *T. boeoticum* var. *kurbagalensense* × *T. sinskajae* var. *sinskajae* | *T.boe*.v.*kur* × *T.sin*.v.*sin* |
| 10 | *T. boeoticum* var. *kurbagalensense* × *T. monococcum* var. *monococcum* | *T.boe*.v.*kur* × *T.mon*.v.*mon* |

The research was conducted at the experimental field of the Plant Production Institute named after V. Ya. Yuryev of the National Academy of Agrarian Sciences of Ukraine. To create hybrids, the «single cross» method was used. The accessions were sown on plots placed on strips 1 m wide, in transverse rows with intervals of 15 cm, according to the scheme: mother — father — $F_1$ — $F_2$ — mother — father. There were six rows on the plots of the parental forms. The rows number of hybrids depended on the seed number.

To obtain seeds, parental forms and $F_1$ hybrids were sown in the fall of 2020 and 2021 years. To determine growth habit of the plants of $F_1$ and $F_2$ hybrids and parental forms, they were sown in the spring 2022 what excluded influence of low temperatures as a vernalization factor. The $F_1$ and $F_2$ hybrid generations were evaluated by the growth habit at the end of the growing season (Goncharov, 2012). The plant that move to the shooting phase was classified as spring type, the one that did not come out was classified as winter (Goncharov, 2012). The segregation analysis was performed by the $\chi^2$ method with the Yates' correction.

**Results and discussion**

The table 3 shows that the accessions UA0300401 (*T.boe.*v.*kur*), UA0300336 (*T.boe.*v.*bic*) and UA0300253 (*T.ura.*v.*spon*) developed a rosette of leaves during spring sowing and did not proceed to heading. In the sample UA0300400 (*T.boe.*v.*tha*), at the end of the growing season, 1 % of plants headed, they developed sterile anthers and grains did not set. Both accessions of *T. monococcum* and the accession of *T. sinskajae* were headed during spring sowing, developed normally and produced complete seeds. Thus, the parental forms of the hybrids were characterized by an alternative manifestation of the growth habit.

In the vast majority of cases, in hybrids between wild einkorns *T. boeoticum* and *T. urartu*, which have a winter growth habit, on the one hand, and cultivated einkorns *T. monococcum* and *T. sinskajae*, headed during spring sowing, on the other hand, $F_1$ plants do not go to generative development. The number of headed plants did not exceed 13.8 % (table 3). Moreover, they headed at the end of the growing season, developed sterile anthers and did not set grains. Thus, the winter growth habit dominated in $F_1$.

A growth habit is a complex trait which is determined by at least two genetical systems — *Vrn* and *Ppd*, there are others with a weaker effect (Xiao, He, 2020; Bloomfield et al., 2018). V. V. Zhmurko (2020) showed that the *Vrn* and *Ppd* genes interact in the regulation of wheat development. It is believed that heading of wheat is determined by a complex of genetic and environmental factors, in which the genes responsible for vernalization and photoperiodism play a decisive role (Kiss et al., 2014).

Wild species including *T. boeoticum* and *T. urartu*, are of winter phenotype, but exist as populations in which both systems can be represented by different alleles. At the same time, the dominance of the winter growth habit, characteristic of the above-mentioned wild species, over the spring growth habit, characteristic of the cultivated species *T. monococcum* and *T. sinskajae*, is obvious, despite single late-headed plants in $F_1$. It should be noted that when crossing the winter and spring forms within the cultural species *T. monococcum*, the springness dominates (Goncharov, 2012).

**Table 3. Growth habit of $F_1$ plants**

| Cross No. | Crossing combination | PN | | % *h* | Growth habit |
|---|---|---|---|---|---|
| | | *N* | *h* | | |
| 1 | *T.mon*.v.*mac* × *T.ura*.v.*spon* | 42 | 4 | 9,5 | w |
| 2 | *T.mon*.v.*mac* × *T.boe*.v.*bic* | 39 | 3 | 7,7 | w |
| 3 | *T.sin*.v.*sin* × *T.ura*.v.*spon* | 21 | 1 | 4,8 | w |
| 4 | *T.sin*.v.*sin* × *T.boe*.v.*tha* | 29 | 4 | 13,8 | s-w + w |
| 5 | *T.boe*.v.*tha* × *T.mon*.v.*mon* | 28 | 0 | 0,0 | — |
| 6 | *T.boe*.v.*tha* × *T.sin*.v.*sin* | 33 | 1 | 3,0 | s-w |
| 7 | *T.boe*.v.*tha* × *T.boe*.v.*kur* | 20 | 2 | 10,0 | w |
| 8 | *T.boe*.v.*tha* × *T.mon*.v.*mac* | 29 | 0 | 0,0 | w |
| 9 | *T.boe*.v.*kur* × *T.sin*.v.*sin* | 22 | 0 | 0,0 | — |
| 10 | *T.boe*.v.*kur* × *T.mon*.v.*mon* | 20 | 2 | 10,0 | s-w |

Note: PN — The plant number, *n* — total, *h* —headed plants, w. — winter, s-w — intermediate («semi-winter»).

The results of the hybridological analysis of $F_2$ plants according to the growth habit are presented in the table 4. In $F_2$ of the hybrids between wild and cultivated forms, the segregation according to the trait «winterness / springness» corresponds to 3 : 1 ($\chi^2_{\{3:1\}}$ < 3.84), i.e. the «springness» trait is inherited in a recessive manner, and the difference between the parental forms is monogenic.

In the seventh combination *T.boe.*v.*tha* × *T.boe.*v.*kur*, the ratio «winterness / springness» did not differ statistically significantly from the 15 : 1 ratio ($\chi^2_{\{15:1\}}$ = 3.84; $\chi^2_{actual.}$ = 3.55). It can be assumed that the differences in the growth habit in this combination are controlled by two gene pairs according to the polymer type while winterness is inherited as a dominant trait.

In the fifth (*T.boe.*v.*tha* × *T.mon.*v.*mon*), sixth (*T.boe.*v.*tha* × *T.sin.*v.*sin*), eighth (*T.boe.*v.*tha* × *T.mon.*v.*mac*) and ninth (*T.boe.*v.*kur* × *T.sin.*v.*sin*) combinations segregation corresponds to 13 : 3. This means that the growth habit in these hybrids is controlled by two pairs of genes according to the type of dominant epistasis; in this case, winterness is also a dominant trait.

**Table 4. Segregation in $F_2$ hybrids between einkorn accessions**

| Cross No. | Crossing combination | Plant number in $F_2$ hybrids | | $\chi^2$ ($\chi^2_{critical}$ = 3.84) | | | |
|---|---|---|---|---|---|---|---|
| | | Winter | Spring | 3:1 | 15:1 | 9:7 | 13:3 |
| 1 | *T.mon.v.mac ×T.ura.v.spon* | 134 | 55 | 1.69 | 168.42 | 16.48 | 13.29 |
| 2 | *T.mon.v.mac × T.boe.v.bic* | 137 | 58 | 2.34 | 183.69 | 15.54 | 15.47 |
| 3 | *T.sin.v.sin × T.ura.v.spon* | 160 | 55 | 0.04 | 137.12 | 28.84 | 6.59 |
| 4 | *T.sin.v.sin × T.boe.v.tha* | 145 | 60 | 1.99 | 185.37 | 17.47 | 14.89 |
| 5 | *T.boe.v.tha × T.mon.v.mon* | 140 | 44 | 0.12 | 97.97 | 29.42 | 3.22 |
| 6 | *T.boe.v.tha × T.sin.v.sin* | 157 | 43 | 1.31 | 79.38 | 40.23 | 0.99 |
| 7 | *T.boe.v.tha × T.boe.v.kur* | 193 | 6 | 51.30 | 3.55 | 134.18 | 32.34 |
| 8 | *T.boe.v.tha × T.mon.v.mac* | 161 | 48 | 0.46 | 99.67 | 36.68 | 2.44 |
| 9 | *T.boe.v.kur × T.sin.v.sin* | 151 | 45 | 0.44 | 93.39 | 34.43 | 2.28 |
| 10 | *T.boe.v.kur × T.mon.v.mon* | 156 | 55 | 0.13 | 141.41 | 26.81 | 7.41 |

Dominance and monogenic control of springness in diploid wheat *Triticum monococcum* L. has been shown by a number of authors (Kuspira et al., 1989; Golovnina et al., 2010). According to Goncharov (1999), in tetraploid wheats, springiness dominates over winterness. A similar result was obtained in hexaploid wheats (Davydova et al., 2016).

It is believed that the ancestral wild forms of wheat are of winter growth habit. The recessive allele *vrn 1* is considered to be older than the dominant allele *Vrn 1* (Goncharov et al., 2018). It is assumed that spring einkorns originated in wild populations and were later selected for cultivation This gave reason to believe that in the evolution of wheat there was a transition from recessive winter forms to dominant spring ones. The results of our study indicate that in hybrids between wild and cultivated accessions of einkorn wheat, winterness characteristic of wild forms dominates and the ability to head during spring sowing of cultivated samples is recessive. This gives grounds to reconsider the ways in which the growth habit was formed during the domestication of one of the first cultivated cereals — einkorn wheat.

*Vrn1* and *Vrn2* are the main genes that control the growth habit of wheat and other temperate cereals. These two genes create a strong epistatic effect, probably being part of the same regulatory chain. In diploid wheat (*Triticum monococcum* L.), *Vrn1* dominates as a springiness factor while *Vrn2* dominates as a winterness factor (Yan, 2004). On the other hand, it was found that the *Vrn*-A1b and *Vrn*-A1h alleles, previously described as dominant, either have no or weak association with the spring habit while in some diploid accessions this habit was associated with the recessive *Vrn*-A1 allele (Shcherban et al.

2015). Thus, there is reason to consider an alter-?ative path of evolution: from winterness to the ability to heading at spring sowing.

In the $F_2$ hybrid *T.boe.*v.*tha* × *T.boe.*v.*kur*, segregation meet not to a monogenic control model but rather to a digenic one, where one of the genes of each pair is represented by the dominant allele that determines winterness. It can be supposed that one of the genes is *Vrn*-A1 (Shcherban et al., 2015) and the other is *Vrn*2 (Distelfeld et al., 2008). It is also possible that the gene controlling the photoperiodic reaction is involved.

### Conclusions

1. In the crossings of einkorn wheat wild forms *T. boeoticum* and *T. urartu* with cultivated *T. monococcum* and *T. sinskajae*, the winter growth habit of wild forms dominates over the spring growth habit characteristic for cultivated forms.
2. Differences in «winterness / springness» phenotype between parental forms in crosses of *T. monococcum* var. *macedonicum* with *T. urartu* var. *spontaneorubrum* and *T.boeoticum* var. *bicolor*; *T. sinskajae* var. *sinskajae* with *T. urartu* var. *spontaneorubrum* and *T. boeoticum* var. *thaoudar*; *T. boeoticum* var. *thaoudar* with *T. monococcum* var. *monococcum, T. sinskajae* var. *sinskajae* and *T. monococcum* var. *macedonicum*; *T. boeoticum* var. *kurbagalensense* with *T. sinskajae* var. *sinskajae* and *T. monococcum* var. *monococcum* are controlled by a single gene (monogenically). The difference between the two wild forms in crossing *T. boeoticum* var. *thaoudar* × *T. boeoticum* var. *kurbagalensense* is controlled by two genes. In the crosses *T. boeoticum* var. *thaoudar* with *T. monococcum* var. *monococcum*, *T. sinskajae* var. *sinskajae* and *T. monococcum* var. *macedonicum*; *T. boeoticum* var. *kurbagalensense* × *T. sinskajae* var. *sinskajae*, the parental forms also differ digenously.
3. When domesticating einkorns, the transition from winter to spring forms is associated with a change in the regulation of the genes' action, their manifestation in a heterozygote from a dominant state to a recessive one.

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## УСПАДКУВАННЯ ТИПУ РОЗВИТКУ У ПШЕНИЦЬ ОДНОЗЕРНЯНОК

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**Мета.** З'ясувати характер успадкування ознаки «озимість / ярість» у гібридів між представниками видів пшениць однозернянок. **Методи.** Схрещування проводили методом «single cross». Характер успадкування типу розвитку визначали за допомогою гібридологічного аналізу. **Результати.** Показано, що при гібридизації диких форм пшениці *T. boeoticum* та *T. urartu* з культурними *T. monococcum* та *T. sinskajae* озимий тип розвитку диких форм домінує над ярим, властивим культурним формам. Відмінність за фенотипом «озимість / ярість» між зразками у схрещуваннях *T. monococcum* var. *macedonicum* з *T. urartu* var. *spontaneorubrum* та *T. boeoticum* var. *bicolor*; *T. sinskajae* var. *sinskajae* з *T. urartu* var. *spontaneorubrum* та *T. boeoticum* var. *thaoudar*; *T.boeoticum* var. *thaoudar* з *T. monococcum* var. *monococcum*, *T. sinskajae* var. *sinskajae* та *T. monococcum* var. *macedonicum*; *T. boeoticum* var. *kurbagalensense* з *T. sinskajae* var. *sinskajae* та *T. monococcum* var. *monococcum* контролюється одним геном. Відмінність між двома дикими формами у схрещуванні *T. boeoticum* var. *thaoudar* × *T. boeoticum* var. *kurbagalensense* контролюється двома генами. Дигенно відрізняються також батьківські форми у схрещуваннях *T. boeoticum* var. *thaoudar* з *T.monococcum* var. *monococcum*, *T. sinskajae* var. *sinskajae* та *T. monococcum* var. *macedonicum*; *T. boeoticum* var. *Kurbagalensense* × *T. sinskajae* var. *sinskajae*. **Висновки.** Озимість диких форм пшениці однозернянки домінує над ярістю культурних її форм. Відмінності за типом розвитку «озимість / ярість» між вивченими формами однозернянки обумовлені 1–2 парами генів.

**Ключові слова:** пшениця однозернянка, тип розвитку, озимість, ярість, успадкування.