Vernalisation Response of Some Winter Wheat Cultivars (*Triticum aestivum* L.)

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Abstract: For 17 cultivars of winter wheat (*Triticum aestivum* L.) different vernalisation and photoperiod responses were detected. The effect of photoperiod sensitivity was not significantly changed by vernalisation; different vernalisation responses were probably due to the presence of multiple alleles at *Vrn* loci. The delay in heading depended on the vernalisation deficit exponentially: y = parameter (1) + [y_0 – parameter (1)] × EXP [parameter (2) × ($x - x_0$)]. The dependence was shown to be general and significant for the given model in all the studied cultivars. Individual regressions characterised responses of cultivars to a deficit of vernalisation treatment. Cluster analysis according to the characterisation obtained (full vernalisation requirement, minimum vernalisation requirement, insufficient vernalisation and parameters of the dependence) showed the relationships between cultivars and enabled their grouping by similar profiles of vernalisation, and, possibly, of photoperiod response. In individual cultivars, an attempt was made to use the model to predict performance for some agronomic traits.

Keywords: *Triticum aestivum*; wheat; *Vrn* genotypes; vernalisation response; time to heading

Different sensitivity of wheat varieties to vernalisation is decisive for their growth habit. Low requirement or the absence of requirement is characteristic of spring growth habit while a long period of cold treatment is required by winter wheat. If the requirement for vernalisation is not met, heading of plants is inhibited.

The vernalisation response of wheat is genetically determined by the genes *Vrn-A1*, *Vrn-B1* and *Vrn-D1*, earlier designated *Vrn1*, *Vrn2* and *Vrn3* (MCINTOSH *et al.* 1998), each having two or more allelic forms (PUGSLEY 1971; SNAPE *et al.* 1976). Spring growth habit demonstrates the presence of at least one dominant *Vrn*, spring type, allele in the genotype.

Winter cultivars have recessive, *vrn,* alleles at all *Vrn* loci (PUGSLEY 1972). The vernalisation requirement of winter wheat is high, but differs among cultivars, which can be explained by the presence of different recessive alleles at the *Vrn* loci (PUGSLEY 1971) or as the effect of modifying genes in the genetic constitution (GOTOH 1980, 1983). KOŠNER and PÁNKOVÁ (1998) noted the presence of different recessive alleles – multiple alleles of recessive *vrn* genes on chromosomes 5A, 5B, 5D (LAW *et al.* 1976; MAISTRENKO 1980).

Growth habit can be changed by the substitution of different dominant and recessive alleles, and thus spring forms can be transformed into winter types (KOŠNER & PÁNKOVÁ 2001a). The changed combinations of different recessive alleles of winter wheat can also affect growth stages, and thus agronomic traits (KOŠNER & PÁNKOVÁ 1999, 2001b).

The aim of this experiment was to detect and characterise vernalisation response within a set of winter wheat cultivars. We evaluated the requirement for full vernalisation, i.e. when all plants headed without significant delay; minimum vernalisation requirement that allowed heading of all plants, although delayed; and insufficient vernalisation when no plants headed; and parameters of an exponential equation expressing the dependence of time to heading on vernalisation deficit.

MATERIAL AND METHODS

17 cultivars of winter wheat (*Triticum aestivum* L.) were chosen from the world collection of the Gene bank, Research Institute of Crop Production (RICP) Prague:

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Austria – Ludwig; Czech Republic – Alana, Brea, Nela, Niagara, Sulamit, Šárka, Vlasta; France – Apache, Corsaire; Germany – Complet, Drifter, Record, Sepstra; Great Britain – Rialto; the Netherlands – Semper; Slovakia – Solara. All the selected cultivars are registered for growing in the Czech Republic.

Seeds of the studied cultivars were germinated at weekly intervals and vernalised at a temperature of +1°C to +3°C, so that periods of 8, 7, 6, 5, 4, and 3 weeks of vernalisation would be achieved on 24 April. After this treatment all plants were set out so that the date of sowing would ensure natural long day conditions with no additional vernalisation in the latitude 50° of the experiment.

Time to heading of plants was measured from 24 April, and heading date was considered the day when the first spike on the main tiller emerged half-way from the boot. Acquired data were processed statistically. The requirement for full vernalisation was expressed by the number of weeks of vernalisation needed for the heading of all plants included in the treatment without significant delay. The minimum requirement for vernalisation was the minimum number of weeks of vernalisation sufficient for heading of all plants though with significant delay, verified by *t*-test again. Insufficient vernalisation was the number of weeks of vernalisation that did not result in heading of any plant. The significance was verified by *t*-test between each of the treatments and the 8-week period of vernalisation.

The response to a deficit of vernalisation was evaluated by regression analysis, and differences between regressions for heading time were found using cluster analysis (Square Euclid; the mean of the groups), focused on all the studied characteristics (full vernalisation requirement, minimum vernalisation requirement, insufficient vernalisation, parameters of the regression equation).

RESULTS AND DISCUSSION

The mean time to heading of the cultivars in all vernalisation treatments is summarised in Table 1 together with statistical characteristics. The data in bold indicate an insignificant difference from the treatment with 8-week vernalisation. In the treatment where not all plants went to heading, percentages of non-heading plants are given. The data show that there are considerable differences between the cultivars in earliness represented by the time to heading under 8-week vernalisation, and in their response to a vernalisation deficit.

Table 2 lists the basic characteristics of vernalisation response for each cultivar, showing the differences between the genotypes: Earliness (= time to heading under 8-week vernalisation), full vernalisation requirement, min-

Table 1. Average days from planting to heading of the studied winter cultivars in all variants of vernalisation, and their basic statistical evaluation

Cultivar	Weeks of vernalisation								
	8	7	6	5	% non heading	4	% non heading	3	% non heading
Alana	**66.70 ± 1.9**	**68.13 ± 1.9**	**68.50 ± 1.3**	71.17 ± 1.1	0.00	80.27 ± 1.8	0.00	95.78 ± 8.3	43.75
Apache	**57.73 ± 1.8**	**61.90 ± 2.0**	62.64 ± 2.4	66.71 ± 2.1	0.00	70.31 ± 2.2	0.00	89.00 ± 5.7	42.86
Brea	**66.06 ± 1.4**	**64.89 ± 1.3**	69.95 ± 1.7	83.50 ± 2.6	0.00	95.00 ± 4.2	20.69	× ± ×	100.00
Complet	**68.56 ± 1.9**	**67.94 ± 1.9**	**68.11 ± 1.4**	**69.63 ± 1.2**	0.00	74.66 ± 1.8	0.00	97.17 ± 8.5	57.14
Corsaire	**68.88 ± 1.1**	**70.45 ± 1.5**	72.67 ± 1.5	77.53 ± 2.4	0.00	95.54 ± 2.8	35.14	× ± ×	100.00
Drifter	**70.68 ± 1.2**	**69.91 ± 1.6**	**71.71 ± 1.2**	76.91 ± 1.3	0.00	89.24 ± 3.1	0.00	100.40 ± 8.5	73.64
Ludwig	**68.56 ± 3.0**	**69.13 ± 1.1**	75.08 ± 2.1	90.65 ± 3.7	0.00	100.50 ± 3.2	45.45	× ± ×	100.00
Nela	**67.68 ± 1.7**	**65.87 ± 1.3**	**68.48 ± 1.3**	79.38 ± 3.2	0.00	96.14 ± 2.6	20.00	× ± ×	100.00
Niagara	**68.85 ± 2.0**	**68.69 ± 1.9**	**70.26 ± 1.4**	86.91 ± 5.7	0.00	97.73 ± 3.6	10.34	× ± ×	100.00
Record	**69.14 ± 3.0**	**67.87 ± 4.3**	**69.53 ± 1.9**	70.51 ± 2.1	0.00	80.55 ± 5.4	21.42	× ± ×	100.00
Rialto	**69.13 ± 2.0**	**65.90 ± 1.7**	**71.73 ± 1.8**	73.50 ± 2.1	0.00	93.13 ± 5.1	40.00	103.00 ± 6.2	71.43
Semper	**68.30 ± 1.7**	**69.42 ± 1.4**	71.33 ± 1.6	73.83 ± 1.5	0.00	77.54 ± 2.9	0.00	88.77 ± 3.2	11.43
Sepstra	**69.68 ± 2.7**	**70.80 ± 1.4**	**68.06 ± 0.9**	73.39 ± 1.5	0.00	79.43 ± 1.9	0.00	89.55 ± 3.3	10.81
Solara	**62.00 ± 2.1**	**63.42 ± 1.9**	67.88 ± 2.4	70.85 ± 1.0	0.00	84.87 ± 2.7	0.00	96.25 ± 3.9	66.67
Sulamit	**67.62 ± 1.5**	**69.04 ± 1.9**	73.64 ± 1.6	89.08 ± 2.8	19.15	91.57 ± 8.7	65.00	× ± ×	100.00
Šárka	**59.98 ± 1.4**	**62.11 ± 2.1**	64.15 ± 1.0	66.46 ± 0.7	0.00	74.69 ± 6.8	0.00	91.50 ± 6.5	60.00
Vlasta	**67.51 ± 1.5**	**68.03 ± 1.3**	69.54 ± 1.1	74.52 ± 0.9	0.00	80.57 ± 8.4	0.00	101.33 ± 12.7	76.92

Table 2. Basic characterisation of vernalisation in the studied cultivars

Cultivar	Earliness 8 weeks (days to heading)	Vernalisation requirement (weeks)		
		full	minimum	insufficient
Alana	66.70	6	4	2
Apache	57.73	7	4	2
Brea	66.06	7	5	3
Complet	68.56	5	4	2
Corsaire	68.88	7	5	3
Drifter	70.68	6	4	2
Ludwig	68.56	7	5	3
Nela	67.68	6	5	3
Niagara	68.85	6	5	3
Record	69.14	6	5	3
Rialto	69.13	6	4	2
Semper	68.30	7	4	2
Sepstra	69.68	6	4	2
Solara	62.00	7	4	2
Sulamit	67.62	7	6	3
Šárka	59.98	7	4	2
Vlasta	67.51	7	4	2

imum vernalisation requirement and insufficient vernalisation.

It can be seen from Table 1 that winter wheat plants respond to the unfulfilled vernalisation requirement by a delay of heading that is slight under a small deficit but increases exponentially following a larger deficit. The dynamics of this dependence is expressed in the equation:

$$y = \text{parameter (1)} + [y_0 - \text{parameter (1)}] \times$$
$$\times \text{ EXP [parameter (2)} \times (x - x_0)]$$

where: y_0 = intercept of y
x_0 = intercept of x
x = vernalisation deficit
y = time to heading (fitted value)
parameter (1), (2) = estimates of regression coefficients

The estimates of characteristics of the dependence of time to heading on vernalisation in the studied cultivars [y_0, x_0, parameter (1), parameter (2)] that were obtained by iteration of the equation are summarised in Table 3, together with the significance of fit with a given model. It was high in almost all cases, thus the exponential equation fits the observed variation, and the proposed model is of general validity.

Although the dependence is exponential in all the observed cases, its structure in individual cultivars or groups characterises their response to unfulfilled vernal-

Table 3. The estimates of characteristics of the dependence of time to heading on vernalisation, significance of their fit with given model in the studied cultivars

Cultivar	Intercept *y*	Intercept *x*	Parameter (1)	Parameter (2)	*F* of the model	Significance	*R*-squared
Alana	67	0	66.536	0.119	1063.99	0.00	1.00
Apache	59	0	58.255	0.106	188.77	0.00	0.97
Brea	65	0	61.976	0.086	87.71	0.00	0.97
Complet	67	0	66.957	0.188	679.22	0.00	0.99
Corsaire	69	0	68.570	0.148	1067.07	0.00	1.00
Drifter	70	0	68.424	0.087	172.31	0.00	0.98
Ludwig	68	0	61.700	0.066	81.17	0.00	0.96
Nela	66	0	65.177	0.130	181.80	0.00	0.98
Niagara	68	0	65.633	0.094	50.41	0.01	0.94
Record	68	0	67.964	0.209	135.18	0.00	0.98
Rialto	67	0	64.456	0.079	65.15	0.00	0.94
Semper	68	0	66.947	0.086	404.93	0.00	0.99
Sepstra	69	0	68.517	0.108	126.69	0.00	0.97
Solara	62	0	58.540	0.069	270.61	0.00	0.99
Sulamit	67	0	52.741	0.037	31.80	0.01	0.91
Šárka	60	0	59.015	0.100	899.98	0.00	1.00
Vlasta	67	0	65.241	0.077	1282.80	0.00	1.00

isation. It is supposed that the differences are brought about by different genetic constitutions of the cultivars from the viewpoint of vernalisation response. Thence the parameters of the equation represent important data on vernalisation responses of the cultivars.

The data presented in Table 3, together with the other characteristics of vernalisation requirement (Table 2), constitute the groundwork for a comparison of proximity of the cultivars from the viewpoint of the characteristics of vernalisation response, and for grouping the cultivars to the clusters with similar profiles of vernalisation, and possibly photoperiodic requirements. For that purpose hierarchic cluster analysis was carried out. The proximity of cultivars and mutual distances between them are illustrated in a dendrogram (Fig. 1) where four clusters originated according to the closeness of the cultivars. Categorisation into the groups is shown in Table 4.

Group 1. There is a weak response to vernalisation deficit within the group. All plants headed after four weeks of vernalisation. A marked delay or absence of heading in some plants was found after three weeks of vernalisation (35 days of vernalisation deficit), and a further reduction of vernalisation to two weeks was insufficient for heading of any plant. As regards the earliness, they are medium late cultivars, heading after full vernalisation within 66–71 days, Alana being the earliest and Drifter the latest. The slowest response to a vernalisa-

Table 4. Hierarchic cluster analysis – categorisation of the cultivars into 4 clusters (Measurement: Euclid, Method: Mean among the groups)

Cultivar	Origin	Group
Alana	Czech Republic	1
Complet	Germany	1
Drifter	Germany	1
Rialto	Great Britain	1
Semper	the Netherlands	1
Sepstra	Germany	1
Vlasta	Czech Republic	1
Apache	France	2
Solara	France	2
Šárka	Czech Republic	2
Brea	Czech Republic	3
Corsaire	France	3
Ludwig	Austria	3
Nela	Czech Republic	3
Niagara	Czech Republic	3
Record	Germany	3
Sulamit	Czech Republic	4

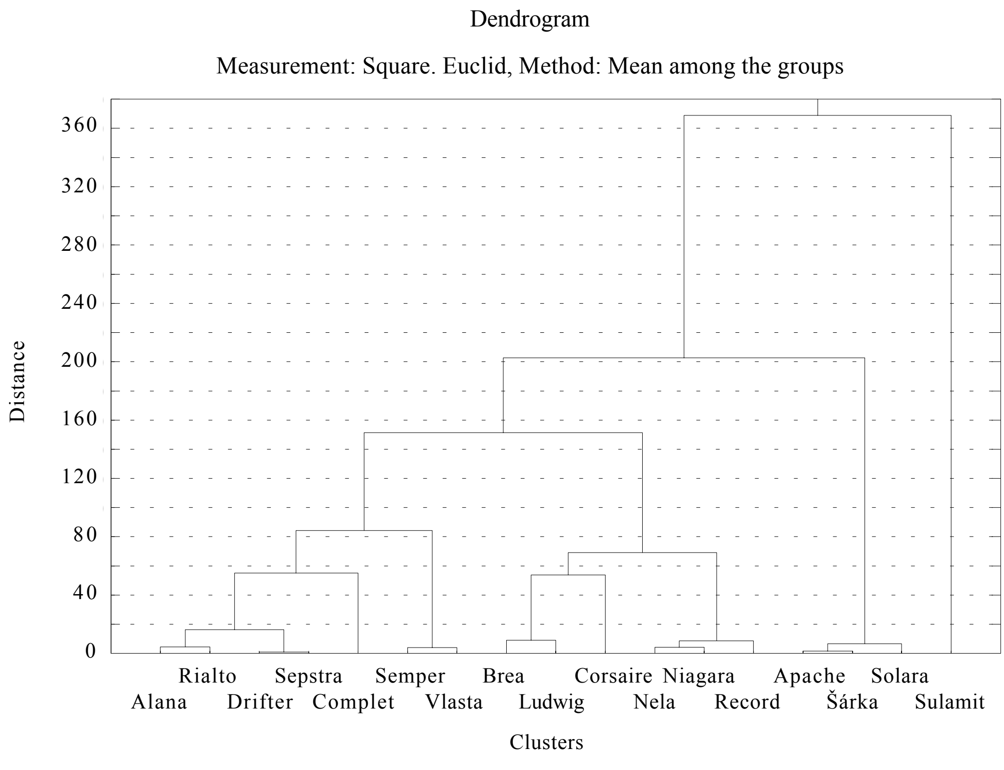

Fig. 1. Hierarchic cluster analysis of all characteristics of response to vernalisation (full vernalisation requirement, minimum vernalisation requirement, insufficient vernalisation and parameters of dependence K1 and K2)

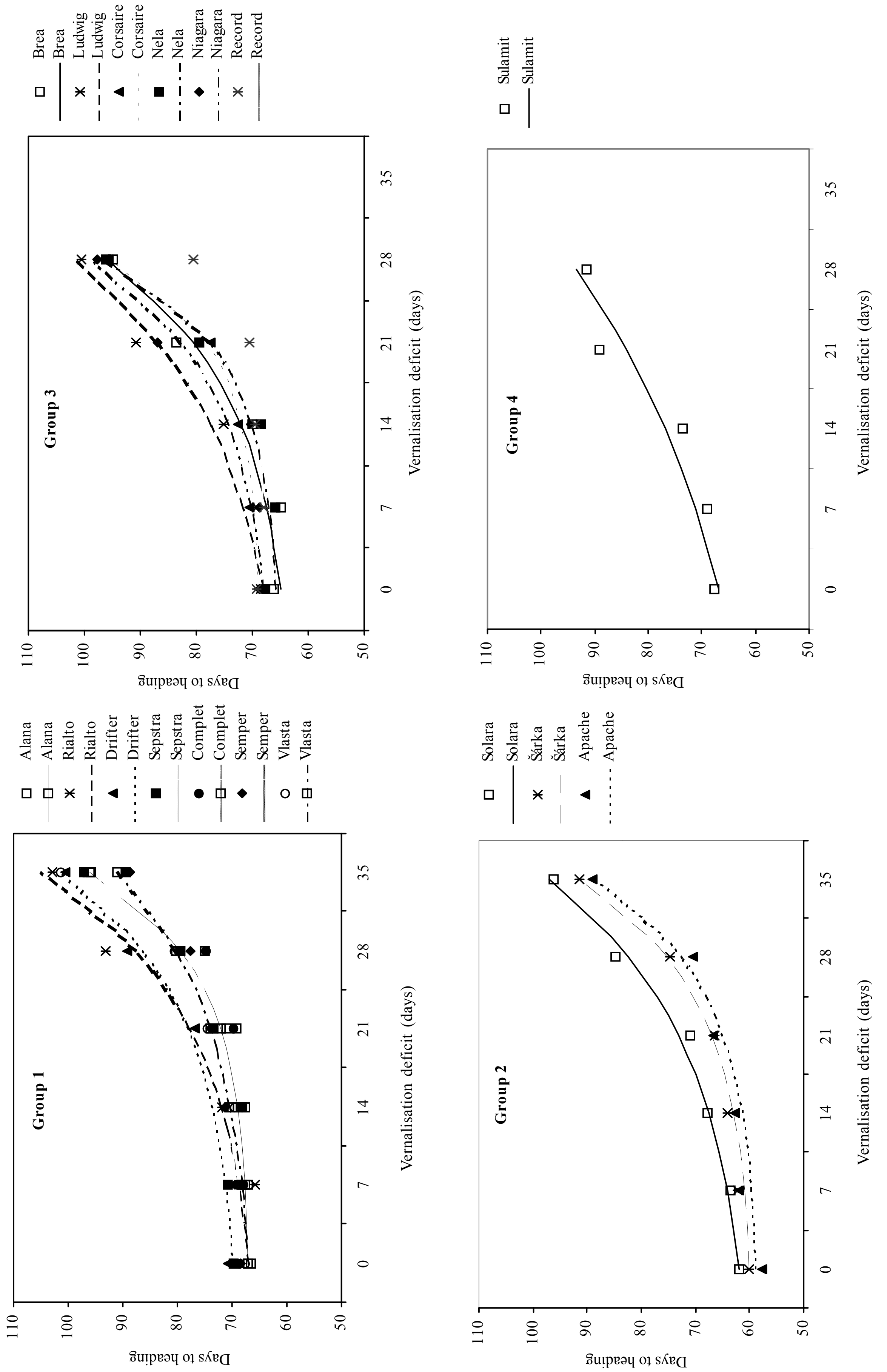

Fig. 2. Regression analysis – dependence of the time to heading on vernalisation (vernalisation deficit)

tion deficit was found in Complet (a significant delay in heading only after a vernalisation deficit longer than three weeks); Rialto responded the most quickly (following a vernalisation deficit longer than one week). We suppose only slight differences in the genetic constitution of vernalisation or photoperiod responses within this group.

As observed earlier, the genetically conditioned vernalisation requirement affects growth stages and agronomic traits (KOŠNER & PÁNKOVÁ 2001) so that we can estimate some characters of the cultivars by analysis of their vernalisation responses. In this case we predict that these cultivars will have a shorter tillering stage, longer stage of stem extension, lower number of tillers and spikes per area, higher number of seeds per spikelet/spike.

Group 2. Three early cultivars with supposedly low photoperiodic sensitivity are included in this group whose heading occurs within 58–62 days after full vernalisation. Their response to vernalisation was not marked: four weeks of vernalisation were sufficient for heading of all plants; a marked delay of heading occurred after three weeks of vernalisation, with a proportion of plants that did not go to heading; two weeks of vernalisation was insufficient for heading. The cultivars responded quickly to a vernalisation deficit, that means one week of vernalisation deficit induced a significant delay in heading. We would not expect any differences in the genetic constitution of *vrn* genes between the cultivars as the dependence of heading on vernalisation deficit was identical within the group. Agronomically, these are predicted to be early cultivars with properties similar to those of Group 1.

Group 3. All cultivars in this group showed a considerable vernalisation requirement. All plants went to heading after five weeks of vernalisation. Three weeks of vernalisation were insufficient for heading of any plant. The response to vernalisation was quick; a significant delay in heading was found following one week of deficit or more. The group comprises medium early cultivars heading within 66 to 69 days after eight weeks of vernalisation; the earliest was Brea, and the latest was Corsaire. It can be predicted in agronomic terms that these would be medium early cultivars that have a longer stage of tillering, shorter stage of stem extension, higher number of tillers and spikes per unit of area, less grains per spike/spikelet.

Group 4. This group consisted of only one medium early cultivar (Sulamit). It responded markedly to a vernalisation deficit; all plants went to heading only after six or more weeks of vernalisation. Three weeks of vernalisation were insufficient for heading of any plant. Agronomically it can be predicted to be analogous to Group 3; possibly more distinct.

The evaluation of the experiment is based on the assumption of the presence of multiple *vrn* alleles of loci *Vrn-A1*, *Vrn-B1* and *Vrn-D1* in the studied cultivars, explaining different vernalisation responses. There is another possible explanation of different vernalisation responses in winter wheat cultivars as the effects of modifying genes (GOTOH 1980, 1983). However, the present experiment supports the idea of multiple alleles (PUGSLEY 1971; KOŠNER & PÁNKOVÁ 1998).

Different heading times with the same equation of response to vernalisation can be explained by different photoperiodic sensitivities, mostly due to different genes *Ppd* present on the homoeologous group 2 chromosomes. The effect of photoperiodic sensitivity on heading time or earliness was described earlier under fully satisfied vernalisation requirements (KOŠNER & ŽŮRKOVÁ 1996). Photoperiodic sensitivity was shown to be one of the main factors influencing earliness represented by the time to heading, and photoperiod sensitive genotypes headed significantly later under the conditions of satisfied vernalisation requirement even though they were grown under long natural photoperiods (longer than 14 hours). In the present experiment, different times to heading following the same period of vernalisation can be explained by different photoperiodic sensitivities. The slopes of regressions of the cultivars with same responses to vernalisation and different photoperiod responses are parallel. The effect of *vrn* genes is projected into different growth stages, and thus into the values of agronomic traits, as was observed with genetically defined lines of wheat carrying different recessive *vrn* alleles (KOŠNER & PÁNKOVÁ 2001). Similar effects of different dominant *Vrn-A1*, *Vrn-B1* a *Vrn-D1* genes on agronomic traits were found in spring cultivars of wheat in a previous paper (STELMAKH 1993).

Conclusions

The studied genotypes of winter wheat cultivars probably contain different alleles determining vernalisation response. Different vernalisation responses of winter wheat cultivars result from the presence of multiple alleles at the *Vrn* loci. Different combinations of the alleles can give rise to genotypes with higher or lower vernalisation response. Unfulfilled vernalisation manifested itself as a delay or even absence of heading. In general, the delay of heading depended exponentially on the degree of vernalisation deficit. Time to heading is also influenced by different photoperiodic responses of the genotypes; but its effect was not significantly changed by vernalisation.

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Abstrakt

KOŠNER J., PÁNKOVÁ K. (2002): **Reakce na jarovizaci u vybraných odrůd pšenice ozimé** (*Triticum aestivum* L.). Czech J. Genet. Plant Breed., **38**: 97–103.

U souboru 17 odrůd pšenice byla určena potřeba jarovizace a reakce na deficit jarovizace. Bylo zjištěno, že sledované odrůdy mají rozdílné jarovizační nároky. Na dobu do metání měla rovněž vliv fotoperiodická citlivost genotypů; její vliv se jarovizací významně neměnil. Nestejná potřeba jarovizace je pravděpodobně způsobována rozdílnými alelami *vrn* (mnohotným alelomorfismem). Prodloužení doby do metání bylo závislé na deficitu jarovizace a závislost měla exponenciální charakter podle rovnice: y = parametr (1) + [y_0 – parametr (1)] × EXP [parametr (2) × ($x - x_0$)]. Průběh závislosti měl obecný charakter a významnost pro daný model byla u všech sledovaných odrůd průkazná. Regresní křivky vystihují reakci jednotlivých odrůd či skupin odrůd na deficit jarovizace. Použitím shlukové analýzy podle všech zjištěných charakteristik jarovizace (plná potřeba jarovizace, minimální potřeba jarovizace, nedostatečná jarovizace a parametry rovnice závislosti) byla určena spřízněnost odrůd a odrůdy byly seskupeny do skupin s podobným profilem jarovizačních, případně fotoperiodických nároků. U jednotlivých skupin odrůd byl učiněn pokus o predikci některých agronomických znaků.

Klíčová slova: *Triticum aestivum*; pšenice; *Vrn*-genotypy; jarovizační reakce; doba metání

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