

## The Effect of Chromosome 3B Gene/s of Česká Přesívka on Vernalisation Response, Photoperiod Sensitivity and Earliness of Wheat

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**Abstract:** Substitution lines with the chromosome 3B of the Czech alternative cultivar Česká Přesívka (CP) in the genetic background of the wheat cultivars Zdar, Vala, Košutka, Jara and Sandra, differing in their requirements of vernalisation and photoperiod, were compared with the original cultivars under short and long photoperiod, to evaluate the effects of genes, located on the chromosome 3B of CP, on earliness and the response to photoperiod and vernalisation. The results suggest that these genes have only a small effect upon the vernalisation requirement, but are more related to the response to photoperiod. However, the genes on the substituted chromosome appear to influence the earliness *per se* and very likely interact also with the photoperiodic response.

**Keywords:** *Triticum aestivum*; wheat; *Vrn*; vernalisation response; *Ppd*; photoperiod response; earliness *per se*

The outstanding adaptability of wheat makes its cultivation possible at almost any agricultural climate on earth. This is possible due to a wide range of genetically based photoperiod and vernalisation responses. In addition, genes for earliness *per se* can also affect growth and development (SCARTH & LAW 1984). The response to the photoperiod is manifested in the duration of individual phases of growth and development. Common wheat is generally classified as a long-day plant (VINCENCE-PRUE 1975), but the currently grown cultivars show a wide range of photoperiodic sensitivity and thus a wide range of adaptation. Wheat cultivars grown at high latitudes usually require long day photoperiods, while wheat cultivars grown at lower latitudes tend to be less sensitive to the photoperiod or insensitive.

Photoperiodic sensitivity is genetically controlled by three loci designated *Ppd-D1*, *Ppd-B1*, *Ppd-A1*, located on the chromosomes 2D, 2B and 2A, respectively (WELSH *et al.* 1973; SCARTH & LAW 1983). Insensitivity is dominant over sensitivity (PUGSLEY 1966). The effect of individual dominant alleles on the photoperiodic sensitivity is different; *Ppd-D1* acts most markedly and is epistatic to the other alleles, and the effect of *Ppd-B1* is stronger than the effect of *Ppd-A1* (SNAPE *et al.* 1998).

Vernalisation response is also of fundamental importance for the development of wheat. Genes controlling

vernalisation response determine the requirement of a cool period, that the plants need to reach heading, and are thus responsible for the growth habit of wheat. Spring cultivars do not need vernalisation, while winter cultivars need a long period of vernalisation. Genetic differences in growth habit are determined in particular by the genes *Vrn-A1*, *Vrn-B1*, *Vrn-D1*, each with two or more alleles (PUGSLEY 1971; SNAPE *et al.* 1976). Combinations of these genes determine the vernalisation requirement, i.e. the growth habit. Spring growth habit is manifested if a dominant allele *Vrn* is present in the genotype. The dominant allele of the locus *Vrn 1* is epistatic and suppresses completely the vernalisation requirement; the alleles *Vrn-B1* and *Vrn-D1* inhibit it partially. The genes *Vrn-A1*, *Vrn-B1*, *Vrn-D1* are located on chromosomes 5A, 5B, 5D respectively (LAW *et al.* 1976; MAISTRENKO 1980). Other loci are also known to influence the vernalisation requirement, particularly *Vrn 5* on chromosome 7B (LAW 1966). Winter cultivars have a recessive constitution of all three loci (PUGSLEY 1972). They have a strong, but not identical, vernalisation requirement. This can be explained by the presence of other recessive alleles of *Vrn* genes (PUGSLEY 1971; KOŠNER & PÁNKOVÁ 1997), or by modifying genes in the genetic background (GOTOH 1980, 1983). Genes of chromosome groups 2, 3, 4, 6 and 7 can influence the flowering time independently of environ-

mental conditions (WORLAND 1996). Interaction with *Vrn* genes is assumed in the group 6 chromosomes (ISLAM-FARIDI *et al.* 1996). KOŠNER (1987) found by monosomic analysis of the growth habit of the alternative cultivar Česká přesívka (abbr. CP), that also the chromosome 3B considerably delayed the heading, although the dominant allele *Vrn-B1* and the recessive allele *Ppd* were present. The 3B substitution lines in the background of the cvs. Chinese Spring (*Vrn-D1*) and Zlatka (*Vrn-A1*) resisted the winter unlike the original recipient cultivars. In addition, the substitution line in the background of cv. Zlatka was more sensitive to the photoperiod than cv. Zlatka (KOŠNER 1992).

## MATERIALS

Five cultivars, differing in vernalisation and photoperiodic responses, and lines of these, in which the chromosome 3B was substituted with that of CP were used. CP is a Czech wheat landrace of alternate growth habit with outstanding frost hardiness and safely heading after spring sowing. The cultivars were:

- Zdar** – a winter wheat with high vernalisation and photoperiodic response,
- Vala** – a winter wheat with medium vernalisation and photoperiodic response,
- Košutka** – a winter wheat with low vernalisation and photoperiodic response,
- Jara** – a spring wheat with the gene *Vrn-A1* and sensitive to photoperiod,
- Sandra** – a spring wheat with the genes *Vrn-B1* a *Vrn-D1* and sensitive to photoperiod (KOŠNER & BELATKOVÁ 1992; KOŠNER & BROMOVÁ 1993; KOŠNER & PÁNKOVÁ 1997).

The substitution lines have been formed by a series of backcrosses, each followed by a generation of self-pollination, with monosomic lines 3B of the listed cultivars. The monosomic lines originated from monosomic lines of cv. Zlatka, backcrossed to the listed varieties.

## METHODS

The substitution lines and the corresponding cultivars were compared after different duration of vernalisation and at short and long photoperiods.

Grains of the tested lines were germinated at one-week intervals and exposed to temperatures between +1 and +3°C. In this way variants with 8, 7, 6, 5, 4 and 3 weeks of vernalisation were obtained and planted onto experimental plots on 20<sup>th</sup> April. The photoperiod exceeded 14 hours after this date and could be characterised as long days. It was supposed, that after that date additional vernalisation by low temperature did not occur.

Seedlings of the cultivars and substitution lines were planted after 8 weeks of vernalisation on a plot with a

dark cover, that was daily removed from 8 to 18 o'clock, to produce a 10 h photoperiod. The darkening was stopped when the photoperiodically less sensitive Košutka started heading, so that also the photoperiodically more sensitive cultivars could reach heading. The time from germination to heading was recorded. The 20<sup>th</sup> April (date of planting vernalised seedlings) was taken as the date of germination. Heading was recorded when half of the ear on the first tiller of a plant was showing.

The data were statistically evaluated by analysis of variance (ANOVA). The response to vernalisation was expressed as a regression equation, which was non-linear in winter wheat and linear in spring wheat.

## RESULTS

### Vernalisation requirements

The substitution of the chromosome 3B of CP significantly delayed heading in the cultivars Vala, Košutka and Jara, regardless if the vernalisation requirement was satisfied. Significant interaction between genotype and duration of vernalisation was detected only in the cv. Košutka. Contrary effects were noted in the cv. Sandra, where the substitution line headed significantly earlier than the recipient cultivar. No significant differences or interactions were observed between cv. Zdar and its substitution line. Significance was derived from ANOVA of average time to heading in individual variants of vernalisation (Table 1). The significance of differences between the recipient cultivars and the respective substitution lines is shown in Table 2. In winter wheat only those vernalisation variants were evaluated, in which all plants reached heading.

A deficit of vernalisation in winter genotypes (both cultivars and substitution lines) was expressed by delayed or even absence of heading. The delay of heading time by a vernalisation deficit could be described by the non-linear exponential equation:

$$y = \text{parameter (1)} + [y_0 - \text{parameter (1)}] \times \text{EXP} [\text{parameter (2)} \times (x - i_0)]$$

where:  $y$  = time to heading (fitted function)

$x$  = vernalisation deficit

$y_0$  = intercept of  $y$

$x_0$  = intercept of  $x$

parameter (1), (2) = estimates of regression coefficients

In the spring genotypes, vernalisation deficit had a moderate effect, expressed in a linear relationship between decreasing duration of vernalisation and the delay of heading time (Fig. 1). No significant deviation of the regression model from the data could be observed.

The observed effects of chromosome 3B of CP in the background of the tested cultivars (Figs. 1 and 2) and their statistical significance (Tables 1 and 2) can be described as follows:

Table 1. Analysis of variance in the studied genotypes and variants of vernalisation

Source of variability	Sum of squares	Degrees of freedom	Mean square	F	Significance
<b>Zdar – Zdar (ČP 3B)</b>					
Genotypes	1.636	1	1.636	0.017	0.8972
Vernalisation	75635.406	3	25211.802	<b>257.662</b>	0.0000
Interaction genotype × vernalisation	477.820	3	159.273	1.628	0.1835
Explained	76692.610	7	10956.087	111.970	0.0000
Error	24266.355	248	97.848		
Total	100958.965	255	395.918		
<b>Vala – Vala (ČP 3B)</b>					
Genotypes	1021.290	1	1 021.290	<b>19.411</b>	0.0000
Vernalisation	8 8415.728	4	22 103.932	<b>420.125</b>	0.0000
Interaction genotype × vernalisation	227.840	4	56.960	1.083	0.3651
Explained	8 9013.335	9	9 890.371	187.984	0.0000
Error	1 6941.325	322	52.613		
Total	10 5954.660	331	320.105		
<b>Košutka – Košutka (ČP 3B)</b>					
Genotypes	334.590	1	334.590	<b>11.807</b>	0.0007
Vernalisation	34 532.948	4	8 633.237	<b>304.637</b>	0.0000
Interaction genotype × vernalisation	487.216	4	121.804	<b>4.298</b>	0.0022
Explained	35 781.340	9	3 975.704	140.289	0.0000
Error	7 084.856	250	28.339		
Total	42 866.196	259	165.507		
<b>Jara – Jara (ČP 3B)</b>					
Genotypes	1 145.956	1	1 145.956	<b>37.012</b>	0.0000
Vernalisation	3 916.295	8	489.537	<b>15.811</b>	0.0000
Interaction genotype × vernalisation	149.728	8	18.716	0.604	0.7745
Explained	5 008.375	17	294.610	9.515	0.0000
Error	21 920.711	708	30.961		
Total	26 929.085	725	37.144		
<b>Sandra – Sandra (ČP 3B)</b>					
Genotypes	260.275	1	260.275	<b>13.024</b>	0.0003
Vernalisation	2 311.551	8	288.944	<b>14.459</b>	0.0000
Interaction genotype × vernalisation	361.825	8	45.228	<b>2.263</b>	0.0217
Explained	2 837.515	17	166.913	8.352	0.0000
Error	12 769.748	639	19.984		
Total	15 607.263	656	23.792		

**Comparison of the recipient cultivars and the respective substitution line:**

**Zdar:** No significant interaction genotype × vernalisation and no significant difference in time to heading were found, although the regression of heading time on vernalisation appeared steeper in the substitution line.

**Vala:** The regression of heading time on vernalisation was almost identical in both genotypes and no significant interaction genotype × vernalisation was observed.

However, the substitution line headed significantly later.

**Košutka:** The regression of heading time on vernalisation was steeper in the substitution line. This was confirmed by the significant interaction genotype × vernalisation. In general the substitution line headed significantly later.

**Jara:** The regression of heading time on vernalisation was almost identical in both genotypes and no sig-

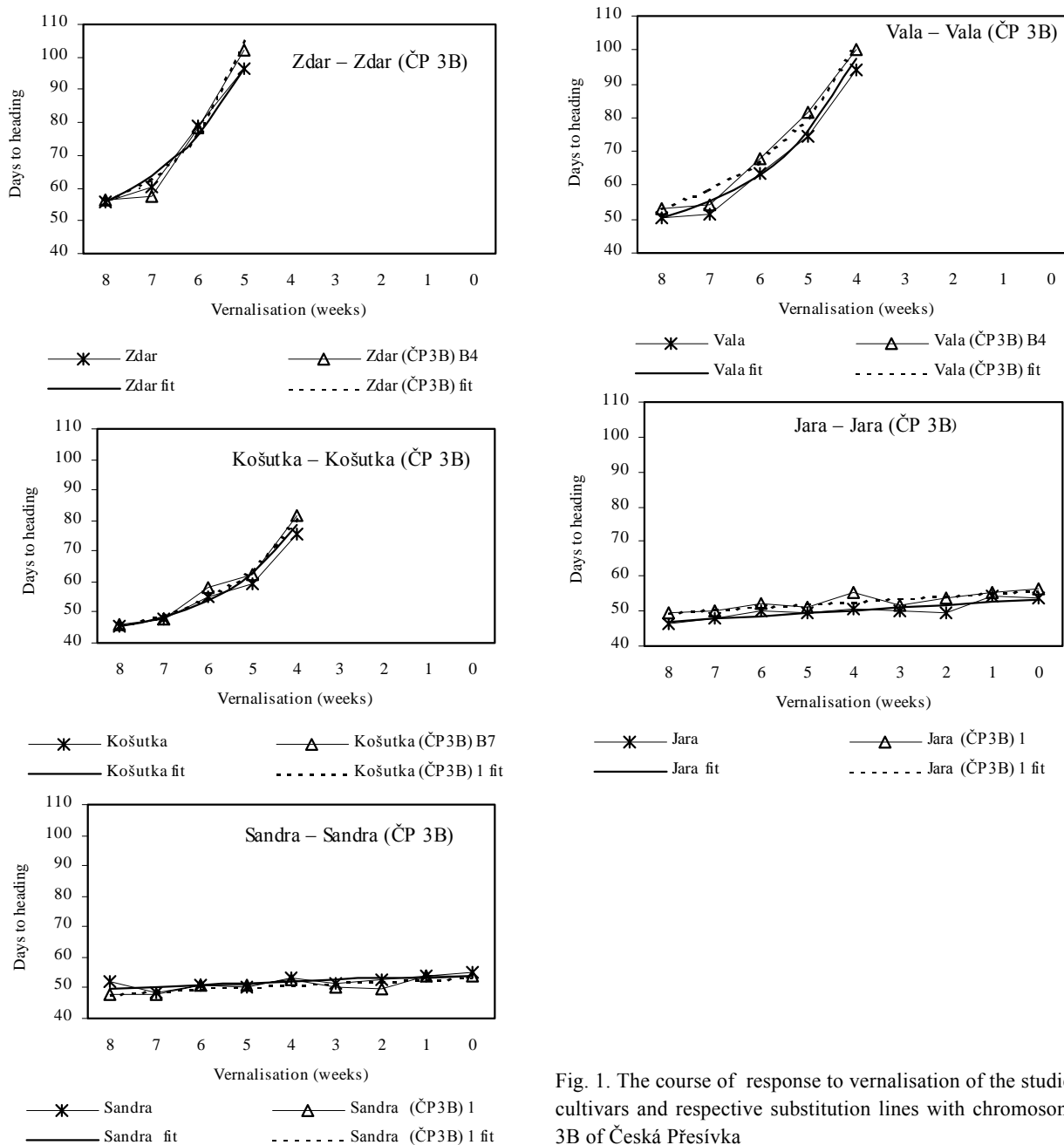


Fig. 1. The course of response to vernalisation of the studied cultivars and respective substitution lines with chromosome 3B of Česká Přesívka

nificant interaction genotype × vernalisation was observed. However, the substitution line headed significantly later.

**Sandra:** The regression of heading time on vernalisation was almost identical in both genotypes, but a interaction was detected between genotype × vernalisation. In contrast to the previous cases, the substitution line headed significantly earlier than the cultivar.

### Response to photoperiod

All studied genotypes were sensitive to day-length and reached heading significantly later at the short 10-hrs

photoperiod. Košutka and Vala and their substitution lines were less sensitive (Table 4 and Fig. 3).

Significant effect of the chromosome 3B of CP on heading time under both long and short days was observed in Košutka and Jara and the respective substitution lines. No significant effect of the chromosome 3B was observed in the cultivars Zdar and Vala. In Sandra the substituted chromosome caused a delay of heading under short day conditions, but an earlier heading under long days. This was statistically expressed as a highly significant interaction genotype × photoperiodic response, but the mean difference between Sandra and its substitution line, though high, was not significant. An interaction between genotype and day-length response

Table 2. Mean time to heading of all variants of vernalisation and significance of differences in time to heading between the recipient cultivar and respective substitution line established by pair *t*-test

Weeks of vernalisation	Zdar	Zdar (ČP3B)	Difference	Vala	Vala (ČP3B)	Difference	Košutka	Košutka (ČP3B)	Difference	Jara	Jara (ČP3B)	Difference	Sandra	Sandra (ČP3B)	Difference
8	55.90	56.23	-0.33	50.44	53.00	-2.56	45.41	45.88	-0.46	46.41	49.52	-3.11	51.85	47.77	4.08
7	60.25	57.30	2.95	51.67	54.00	-2.33	47.56	47.75	-0.19	48.11	50.11	-2.00	48.75	47.83	0.92
6	78.94	78.63	0.32	63.26	68.00	-4.74	55.00	57.93	-2.93	50.00	52.29	-2.29	50.62	50.58	0.04
5	96.26	102.27	-6.01	74.65	81.55	-6.89	59.41	62.21	-2.81	49.57	51.00	-1.43	50.21	50.85	-0.64
4				94.27	100.22	-5.95	75.61	81.54	-5.93	51.42	55.44	-4.02	53.06	52.49	0.57
3										50.19	51.91	-1.73	51.49	50.44	1.05
2										49.61	53.67	-4.05	52.57	49.57	3.00
1										54.07	55.38	-1.30	53.63	54.17	-0.54
0										53.70	56.42	-2.72	55.04	53.69	1.35
Mean time to heading of headed plants and all variants of vernalisation	72.84	73.61		66.86	71.35		56.60	59.06		50.34	52.86		51.91	50.82	
Mean difference between recipient cultivar and substitution line	0.77				4.50	***		2.46	*		2.52	***		-1.09	*
<i>t</i> -test		0.407			4.972			2.374			7.275			-2.091	

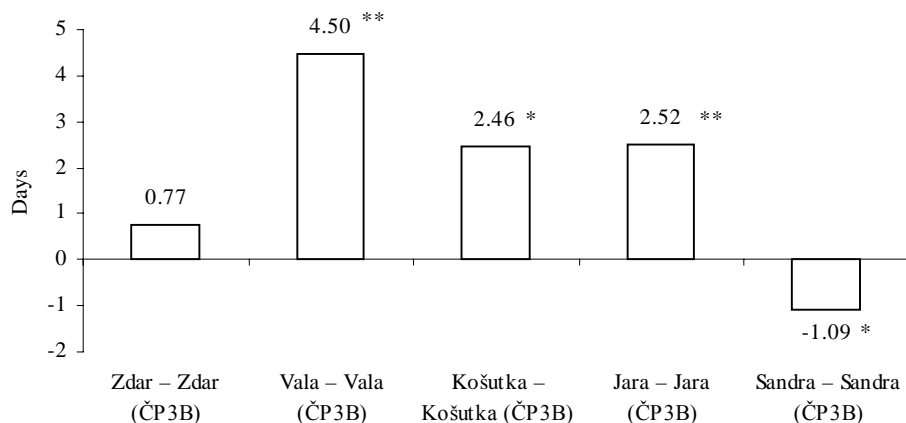


Fig. 2. Mean difference in time to heading between recipient cultivar and substitution line under all variants of vernalisation

at low level of significance was detected also in the comparisons of Vala, Košutka and Jara with their corresponding substitution lines. Significance was assessed by the analysis of variance (Table 3). The effects of genotypes, chromosome substitution, day-length and interactions on heading time are summarised in Table 4. The graphical representations of these effects are given in Figs. 3 and 4.

### DISCUSSION

MIURA and WORLAND (1994) used aneuploid techniques, to show the effects of chromosomes 3B, 3D and 3A on the time to heading. They have found relation-

ships with vernalisation, photoperiod, and earliness *per se*. They used also a substitution line of Chinese spring (CS) with 3B of CP, which without vernalisation and under short day conditions headed later than CS. Our results suggest, that the chromosome 3B of CP significantly affects the time to heading in the substitution lines, except for Zdar where no significant difference was found in any of the parameters studied. It cannot be excluded, however, that in this case accidentally the substituted chromosome was lost due to univalent shift or another reason during formation of the substitution line. In the other substitution lines the time to heading was influenced independently of a deficit in vernalisation.

Since the substituted chromosome influenced the heading time in Sandra in opposite way as in Vala, Ko-

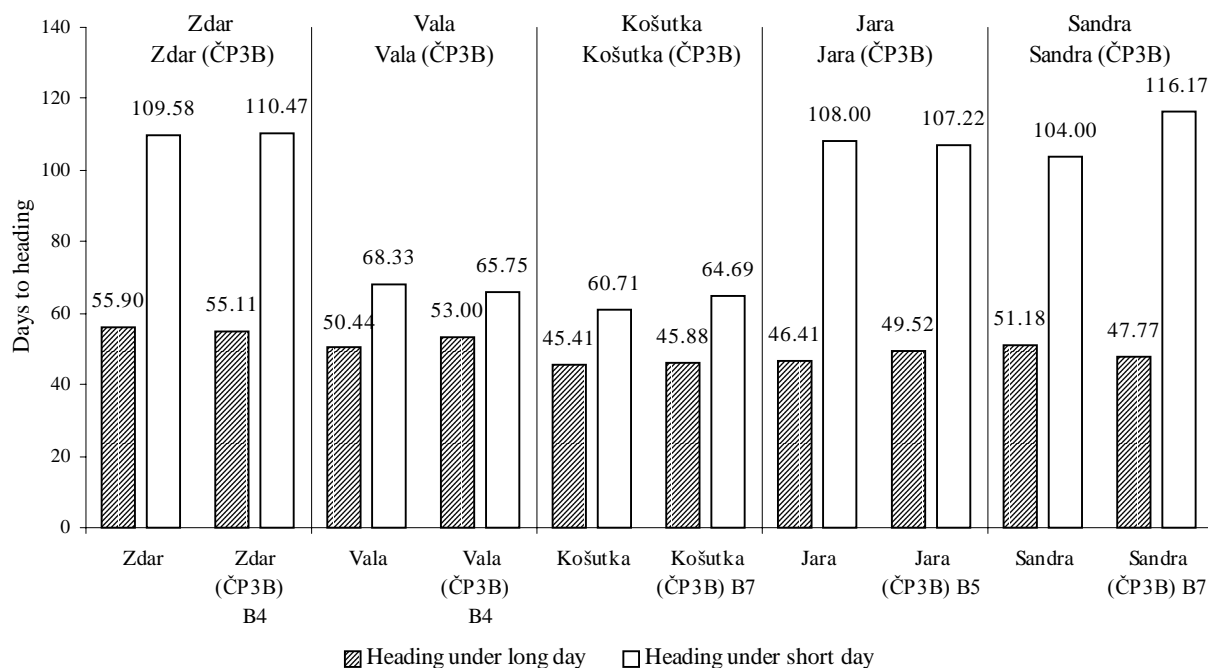


Fig. 3. The response of the studied cultivars and respective substitution lines with 3B chromosome of Česká Přesívka to short (10 h) photoperiod

Table 3. Analysis of variance in the studied genotypes under different photoperiod

Source of variability	Sum of squares	Degrees of freedom	Mean square	F	Significance
<b>Zdar – Zdar (ČP 3B)</b>					
Genotypes	2.905	1	2.905	0.152	0.6975
Photoperiod	57 913.895	1	57 913.895	<b>3029.593</b>	0.0000
Interaction genotype × photoperiod	13.716	1	13.716	0.718	0.3989
Explained	59 684.652	3	19 894.884	1040.742	0.0000
Error	1 949.838	102	19.116		
Total	61 634.491	105	586.995		
<b>Vala – Vala (ČP 3B)</b>					
Genotypes	46.425	1	46.425	1.250	0.2661
Photoperiod	5 338.973	1	5 338.973	<b>143.712</b>	0.0000
Interaction genotype × photoperiod	112.942	1	112.942	<b>3.040</b>	0.0840
Explained	5 499.135	3	1 833.045	49.341	0.0000
Error	4 086.549	110	37.150		
Total	9 585.684	113	84.829		
<b>Košutka – Košutka (ČP 3B)</b>					
Genotypes	62.345	1	62.345	<b>6.394</b>	0.0130
Photoperiod	5 533.145	1	5 533.145	<b>567.441</b>	0.0000
Interaction genotype × photoperiod	57.405	1	57.405	<b>5.887</b>	0.0171
Explained	6 181.888	3	2 060.629	211.324	0.0000
Error	955.602	98	9.751		
Total	7 137.490	101	70.668		
<b>Jara – Jara (ČP 3B)</b>					
Genotypes	203.571	1	203.571	<b>10.910</b>	0.0012
Photoperiod	63 505.361	1	63 505.361	<b>3 403.526</b>	0.0000
Interaction genotype × photoperiod	65.614	1	65.614	<b>3.517</b>	0.0630
Explained	63 774.547	3	21 258.182	1 139.317	0.0000
Error	2406.972	129	18.659		
Total	66 181.519	132	501.375		
<b>Sandra – Sandra (ČP 3B)</b>					
Genotypes	45.035	1	45.035	1.730	0.1915
Photoperiod	51 914.909	1	51 914.909	<b>1 993.933</b>	0.0000
Interaction genotype × photoperiod	922.076	1	922.076	<b>35.415</b>	0.0000
Explained	55 024.353	3	18 341.451	704.453	0.0000
Error	2577.608	99	26.036		
Total	57 601.961	102	564.725		

šutka and Jara, the genes on chromosome 3B of CP probably do not control the vernalisation response. Conversely MIURA and WORLAND (1994) found, that in contrast to CS the CS-substitution line with 3B of CP responded to unfulfilled vernalisation with delayed heading.

The significant interaction genotype × photoperiod in all studied genotypes, except Zdar, suggests, that chromosome 3B of CP affects the response to day-length. It

is interesting, that the Sandra substitution line has a much delayed heading time under short day conditions, but an earlier heading under long days, unlike the other studied genotypes. MIURA and WORLAND (1994) detected a response to short days in the non-vernalised CS substitution line with 3B of CP, where both interactions with the response to day-length and vernalisation were significant. The Zlatka substitution line was more sensitive to the photoperiod than Zlatka (KOŠNER 1992).

Table 4. Time to heading of the studied genotypes under natural long (over 14 h) and short (10 h) photoperiod (Average  $\pm$  conf.l.)

Level		Zdar – Zdar (ČP3B)	Vala – Vala (ČP3B)	Košutka – Košutka (ČP3B)	Jara – Jara (ČP3B)	Sandra – Sandra (ČP3B)
Recipient cultivar	long day	55.90 $\pm$ 1.44	50.44 $\pm$ 1.32	45.41 $\pm$ 0.54	46.41 $\pm$ 0.90	51.85 $\pm$ 2.01
	short day	109.58 $\pm$ 2.49	68.33 $\pm$ 3.13	60.71 $\pm$ 3.21	108.00 $\pm$ 1.95	104.00 $\pm$ 1.32
Substitution line	long day	55.11 $\pm$ 1.50	53.00 $\pm$ 3.08	45.88 $\pm$ 0.58	49.52 $\pm$ 1.44	47.77 $\pm$ 1.35
	short day	110.47 $\pm$ 1.27	65.75 $\pm$ 4.81	64.69 $\pm$ 1.64	107.22 $\pm$ 4.92	116.17 $\pm$ 6.06
Difference of genotypes		0.04	–0.01	2.23**	1.17**	4.04
Effect of photoperiod		54.52****	15.32****	17.06****	59.65****	60.27****
Interaction genotype $\times$ photoperiod		0.84	–2.57*	1.76**	–1.95*	8.12****

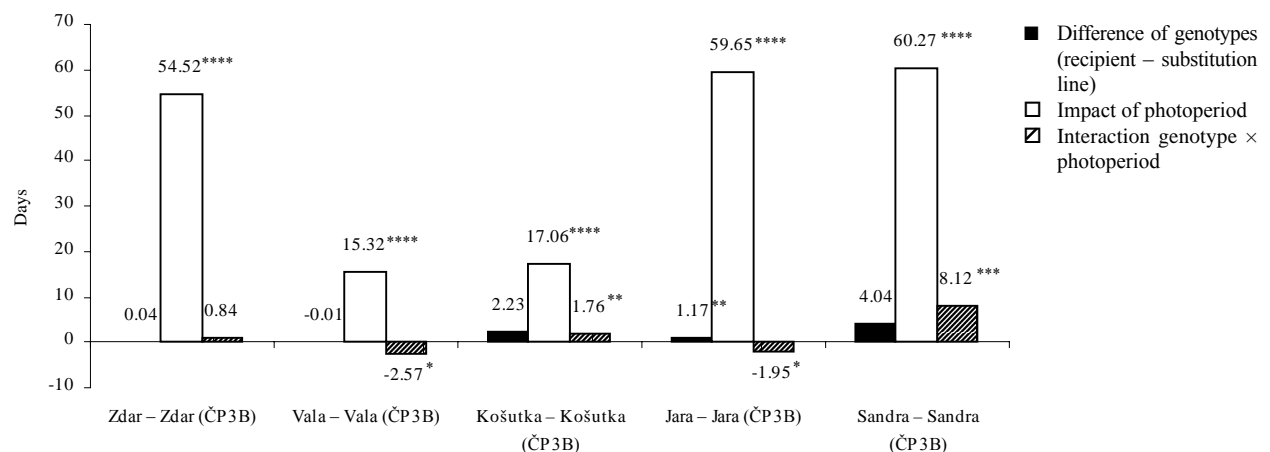


Fig. 4. Mean differences in time to heading under long and short day as effect of genotypes, photoperiod and interactions between genotype and photoperiod

The substitution of the chromosome 3B in CS (*Vrn-D1*) and in Zlatka (*Vrn-A1*) by that of CP resulted in winter survival after autumn sowing, contrary to the recipient cultivars (KOŠNER 1987). Genes on chromosome 3B of CP control more likely the response to the photoperiod than to vernalisation. There are, however, strong indications, that the chromosome 3B contains one or more genes, that affect earliness *per se* and possibly also interact with the response to the photoperiod.

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## Abstrakt

KOŠNER J., PÁNKOVÁ K. (2002): **Účinek genů lokalizovaných na chromozomu 3B odrůdy Česká Přesívka na jarovizační reakci, fotoperiodickou citlivost a ranost pšenice.** *Czech J. Genet. Plant Breed.*, **38**: 41–49.

Při dřívějších studiích genetického založení přesívkového typu pšenice odrůdy Česká Přesívka (KOŠNER 1987) byl kromě působení genů systému *Vrn* a *Ppd* na růst a vývoj zjištěn i vliv chromozomu 3B. K analýze působení genu (nebo genů) na tomto chromozomu byly ve vybraných odrůdách pšenice (Zdar, Vala, Košutka, Jara a Sandra), lišících se v nárocích na jarovizaci a fotoperiodu, vytvořeny substituční linie se substitucí tohoto chromozomu do jejich genetického pozadí. Jak u výchozích odrůd, tak u příslušných substitučních linií byla sledována doba do metání při různých variantách jarovizace (8, 7, 6, 5, 4, 3, 2, 1 a 0 týdnů jarovizace) a při dlouhém a krátkém světelném dni. Z výsledků je zřejmé, že chromozom ČP 3B má značný vliv na růst a vývoj studovaných genotypů. Byl prokázán významný vliv na dobu do metání u všech genotypů (kromě genotypu Zdar) bez ohledu na uspokojení jarovizace, což svědčí o tom, že tento gen (nebo geny) není genem řídícím či významně ovlivňujícím jarovizační reakci. Statisticky průkazná interakce mezi genotypem a fotoperiodou všech sledovaných genotypů (kromě Zdaru) naznačuje, že působení tohoto genu se může projevat v souvislosti s délkou dne. Nejpravděpodobnější však je nezávislé působení genu (nebo genů) na chromozomu ČP 3B – ranost *per se* a jeho případná interakce s fotoperiodickou reakcí.

**Klíčová slova:** *Triticum aestivum* L.; pšenice; gen *Vrn*; jarovizační reakce; gen *Ppd*; fotoperiodická citlivost; ranost *per se*

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