Chromosome Substitutions with Dominant Loci *Vrn-1* and their Effect on Developmental Stages of Wheat

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Abstract: Wheat substitution lines which change winter to spring growth habit were obtained due to substitutions of homoeologous group 5 chromosomes carrying dominant genes *Vrn-A1*, *Vrn-B1* and *Vrn-D1* into the genetic backgrounds of the winter varieties Zdar (sensitive to photoperiod) and Košutka (insensitive to photoperiod), and thus replacing the recessive alleles *vrn-A1*, *vrn-B1, vrn-D1* by dominant alleles. The influence of the substituted chromosomes carrying individual loci *Vrn* on developmental stages of wheat was studied. The verified donor wheat varieties of dominant *Vrn* loci were: Zlatka (*Vrn-A1*, chromosome 5A), Česká Přesívka (*Vrn-B1*, chromosome 5B), and Chinese Spring (*Vrn-D1*, chromosome 5D). The six substitution lines were sown in the field on 10 subsequent dates and their developmental stages were checked to study the effect of the substitutions on development. The lines were also grown under short day conditions (10 hours) to evaluate their photoperiod sensitivity. The analysis of results confirmed the marked effect of chromosome 5A carrying the *Vrn-A1* locus on duration of the developmental stages, besides the influence of sowing date and genetic background. The most shortening effect on growth stages was observed in the lines with substitutions of chromosome 5A (*Vrn-A1)* while the least reduction was in the lines with the substituted chromosome 5B (*Vrn-B1)*. The largest difference in heading time, 6.5 days, occurred between the lines with chromosome substitutions carrying *Vrn-A1* and *Vrn-B1* loci. The effect of substitutions with *Vrn-D1* was intermediate.

Keywords: *Triticum aestivum*; wheat; *Vrn*; growth habit; growth stages

The spring or winter growth habit of wheat is genetically determined by the *Vrn* genes, *Vrn -A1*, *Vrn-B1* and *Vrn-D1*, which are located on long arms of chromosomes 5A, 5B, 5D (Law *et al*. 1976; Maistrenko 1980).

Dominant alleles at *Vrn-A1*, *Vrn-B1*, *Vrn-D1* (Pugsley 1971; Snape *et al*. 1976; McIntosh *et al*. 1998), inhibit the need of wheat plants for a cold period before their change to the generative stage – vernalisation, and thus determine the spring habit.

Recessive alleles present at all three loci are characteristic of winter wheat (Pugsley 1972). The vernalisation requirement of winter wheat varieties is strong but diverse. This can be explained by different recessive *vrn* alleles (Pugsley 1971; Košner & Pánková 1998) or by the action of modifying genes in the genetic background (Gotoh 1980, 1983).

Growth stages of the wheat life cycle that follow after the vernalisation requirement is saturated, are related to important agronomical traits. Duration of the stages is influenced by environmental conditions and by a complex of genetic factors determining vernalisation and photoperiod responses, and earliness *per se*. The genes controlling photoperiod response, *Ppd-D1*, *Ppd-B1* and *Ppd-A1*, are located on homoeologous group 2 chromosomes, 2D, 2B and 2A, respectively (Welsh *et al*. 1973; Scarth & Law 1983). The genes, supposedly of earliness *per se*, *Eps* on group 2, 3, 4, 6 and 7 chromosomes are expected to change the flowering time of wheat independently of environmental conditions (Worland 1996). Interaction between *Eps* genes on homoeologous group 6 chromosomes and *Vrn* genes has been suggested by Islam Faridi *et al*. (1996).

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Genetic effects of dominant alleles *Vrn* on heading time and on agronomical traits of wheat were studied by Stelmakh (1993). He supposed a stronger effect of the *Vrn* genotypes than that of the background or environment.

Other genes of agronomic importance have been found on homoeologous group 5 chromosomes, in addition to the *Vrn* genes. The gene *Q* located on 5A chromosome determines the morphology of spike (speltoid shape), the gene *B1* inhibits production of awns. The order of these genes was detected: *centromere – Vrn-A1 – Q – B1*. For the locus *Vrn-A1* linkage was found with RFLP markers *Xbcd450* and *Xrz395* (0.8 cM) and *Xpsr 426* (5.0 cM) (Kato *et al*. 1998).

MATERIAL AND METHODS

The genetically defined lines where we can distinguish between the effects of individual chromosomes carrying different *Vrn* alleles, and the effect of genetic background, were obtained using chromosome substitutions, based on 8 generations of backcrosses involving monosomic lines for specific chromosomes, alternating with generations of self-pollination, under the cytological control of chromosome numbers. The resulting lines with changed growth habit from winter to spring type carry dominant *Vrn* alleles on the homoeologous group 5 chromosomes substituted into genotypes of winter wheat cultivars Zdar and Košutka differing in their photoperiod response.

A field experiment included the following substitution lines: Zdar (Zlatka 5A), Zdar (Česká Přesívka 5B), Zdar (Chinese Spring 5D), Košutka (Zlatka 5A), Košutka (Česká Přesívka 5B), Košutka (Chinese Spring 5D). The analysis of the growth habit of these lines in relation to the substituted *Vrn* loci and thus verification of donors of dominant alleles *Vrn-A1*, *Vrn-B1*, *Vrn-D1* was carried out in a previous experiment (Košner & Pánková 2001).

The wheat materials were sown in two replications in field plots (1 m wide, one plot = two rows with 20 cm span) at weekly intervals (ten sowing dates between 12. 3. and 14. 5.). Growth stages of the plants were evaluated according to the phenology scale of Zadoks *et al*. (1974). Twenty plants were harvested from each plot to evaluate the effect of chromosome substitutions on agronomical traits.

The wheat lines were also grown under short day (ten hours) conditions to evaluate the photoperiod response of the genetic background. The results were biometrically evaluated using analysis of variance (ANOVA). The assessment was mainly directed to the estimation of genetic differences using statistical models where mean values of the averages of genotypes determining differences were compared (Table 1), and significance was established by the pair-wise *t*-tests.

RESULTS AND DISCUSSION

The evaluation of growth stages using three-factor analysis of variance with interaction (the factors: lines with *Vrn*, genetic background, sowing date; interaction: *Vrn* × background, *Vrn* × sowing date) indicated that, mostly, the duration of growth stages was significantly influenced by all the factors. The interaction between *Vrn* and sowing date was highly significant in the stages between sowing and heading, and between sowing and ripening, while at the other stages it was lower or not significant (Table 1).

The estimates of mean genetic differences due to homoeologous group 5 chromosomes (*Vrn*), and estimates of the effects of the genetic background (Zdar vs. Košutka) on growth stages were obtained by subtracting the mean value of the trait of the lines carrying the substituted chromosome (*Vrn* locus*)* from the mean value of this trait of the lines with another substituted chromosome (*Vrn* locus*)*, and, correspondingly, the other combinations were tested for all chromosomes, sowing dates and repetitions. Thus, pure effects of the respective chromosomes (*Vrn* loci), genetic backgrounds and sowing dates on basic or combined growth stages from sowing to ripening were assessed. The significance was established by 2-range pair-wise *t*-tests on the main value (Table 2).

The evaluation of differences for the length of growth stages indicated that, of the effects of *Vrn* loci, the biggest reduction was due to *Vrn-A1*, and the weakest effect of *Vrn-B1*. The differences in the duration of basic and combined stages from sowing to heading or flowering reached 6.5 days; the lines with *Vrn-A1* are earlier by about one week, as depicted in Figures 1 and 2, respectively. But the reduction of the stages was not regular; tillering and elongation growth are the longest but the stage from flowering to ripening is the shortest in the lines with *Vrn-B1*. This fact could bring interesting outcomes for agronomic traits and yield components. The effect of the *Vrn-D1*

Table 1. The effect of *Vrn* genotype, genetic background and sowing dates on growth stages of wheat; analysis of variance

Source of variability		Sowing – start of tillering	Tillering	Stem extension	Heading – flowering	Flowering –ripening	From sowing to			
							sheath filling	heading	flowering	ripening
Genotypes *Vrn*	*F*	3.93	22.66	19.93	0.57	13.75	15.13	119.23	58.18	15.30
	Sign.	0.02	0.00***	0.00***	0.57	0.00***	0.00***	0.00***	0.00***	0.00***
Genetic background	*F*	1.68	5.54	189.81	4.60	66.19	29.75	413.23	166.53	39.47
	Sign.	0.20	0.02	0.00***	0.04**	0.00***	0.00***	0.00***	0.00***	0.00***
Sowing dates	*F*	63.75	64.60	27.46	1.25	6.68	44.30	270.83	145.26	306.79
	Sign.	0.00	0.00	0.00***	0.28	0.00***	0.00***	0.00***	0.00***	0.00***
Interaction										
Vrn × background	*F*	12.84	3.50	15.53	0.19	14.29	16.91	101.06	54.81	20.96
	Sign.	0.00	0.03	0.00***	0.83	0.00***	0.00***	0.00***	0.00***	0.00***
Vrn × sowing date	*F*	1.10	3.05	1.85	0.89	0.57	0.61	2.73	1.60	2.53
	Sign.	0.37	0.00	0.03**	0.59	0.91	0.89	0.00***	0.08*	0.00***
Background × sowing date	*F*	0.78	2.68	2.09	1.73	2.03	3.07	7.03	2.26	1.12
	Sign.	0.63	0.01	0.04**	0.10*	0.05**	0.00***	0.00	0.03**	0.36

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

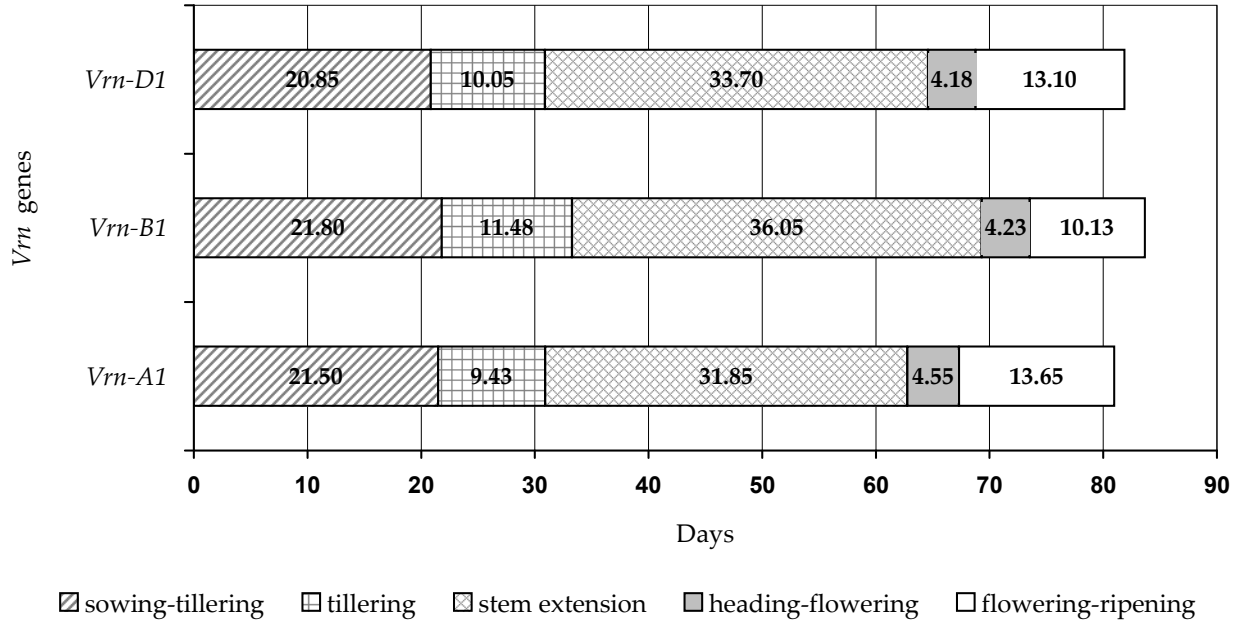

Figure 1. The effect of dominant genes *Vrn* on growth stages

Table 2. Estimates of genetic differences and their evaluation

Source of variability		Sowing – start of tillering	Tillering	Stem extension	Heading – flowering	Flowering – ripening	From sowing to sheath filling	From sowing to heading	From sowing to flowering	From sowing to ripening
Genotypes										
Vrn-A1 – Vrn-B1	***Vrn-A1***	**21.50**	**9.43**	**31.85**	**4.55**	**13.65**	**55.40**	**62.78**	**67.23**	**80.98**
	Vrn-B1	**21.80**	**11.48**	**36.05**	**4.23**	**10.13**	**61.10**	**69.33**	**73.55**	**83.68**
	difference	**–0.30**	**–2.05**	**–4.20**	**0.33**	**3.53**	**–5.70**	**–6.55**	**–6.33**	**–2.70**
	t stat	–0.57	–4.76	–3.80	0.82	4.82	–5.06	–5.59	–4.91	–3.07
	sign.	0.57	0.00***	0.00***	0.42	0.00***	0.00***	0.00***	0.00***	0.00**
Vrn-A1 – Vrn-D1	***Vrn-A1***	**21.50**	**9.43**	**31.85**	**4.55**	**13.65**	**55.40**	**62.78**	**67.23**	**80.98**
	Vrn-D1	**20.85**	**10.05**	**33.70**	**4.18**	**13.10**	**58.08**	**64.60**	**68.55**	**81.88**
	difference	**0.65**	**–0.63**	**–1.85**	**0.38**	**0.55**	**–2.68**	**–1.83**	**–1.33**	**–0.90**
	t stat	1.85	–1.81	–2.96	1.05	0.90	–2.68	–2.69	–1.65	–1.54
	sign.	0.07*	0.08*	0.01***	0.30	0.37	0.01**	0.01**	0.11	0.13
Vrn-B1 – Vrn-D1	*Vrn-B1*	21.80	11.48	36.05	4.23	10.13	61.10	69.33	73.55	83.68
	Vrn-D1	20.85	10.05	33.70	4.18	13.10	58.08	64.60	68.55	81.88
	difference	0.95	1.43	2.35	0.05	–2.98	3.03	4.73	5.00	1.80
	t stat	2.93	3.98	3.19	0.15	–5.08	2.96	7.01	6.73	3.63
	sign.	0.01***	0.00***	0.00***	0.88	0.00***	0.01***	0.00***	0.00***	0.00***
Genetic background										
Long day Zdar – Košutka	**Zdar**	**21.57**	**10.02**	**37.62**	**3.98**	**10.27**	**60.50**	**69.20**	**73.03**	**83.45**
	Košutka	**21.20**	**10.62**	**30.12**	**4.65**	**14.32**	**55.88**	**61.93**	**66.52**	**80.90**
	difference	**0.37**	**–0.60**	**7.50**	**–0.67**	**–4.05**	**4.62**	**7.27**	**6.52**	**2.55**
	t stat	1.03	–1.88	10.04	–2.21	–6.33	4.15	8.75	7.36	4.70
	sign.	0.31	0.06	0.00***	0.03**	0.00***	0.00***	0.00***	0.00***	0.00***
Short day Zdar – Košutka	**Zdar**	**21.00**	**8.00**	**71.33**	**4.67**	**26.33**	**95.67**	**100.33**	**105.00**	**131.33**
	Košutka	**21.00**	**8.00**	**47.33**	**6.67**	**10.67**	**71.33**	**76.33**	**83.00**	**93.67**
	difference	**0.00**	**0.00**	**24.00**	**-2.00**	**15.67**	**24.33**	**24.00**	**22.00**	**37.67**
	t stat			3.95	–1.15	6.02	4.82	3.95	4.16	5.12
	sign.			0.06*	0.37	0.03**	0.04**	0.06*	0.05**	0.04**

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

locus was intermediate, rather nearer to *Vrn-A1* than to *Vrn-B1*.

In addition to the effects of the substituted chromosomes (loci *Vrn*), we can suppose that there is a considerable influence of genetic background. The cultivars Košutka and Zdar differ in their photoperiod responses, Košutka being insensitive while Zdar is highly sensitive to day length (Košner & Belatková 1992; Košner & Pánková 1997).

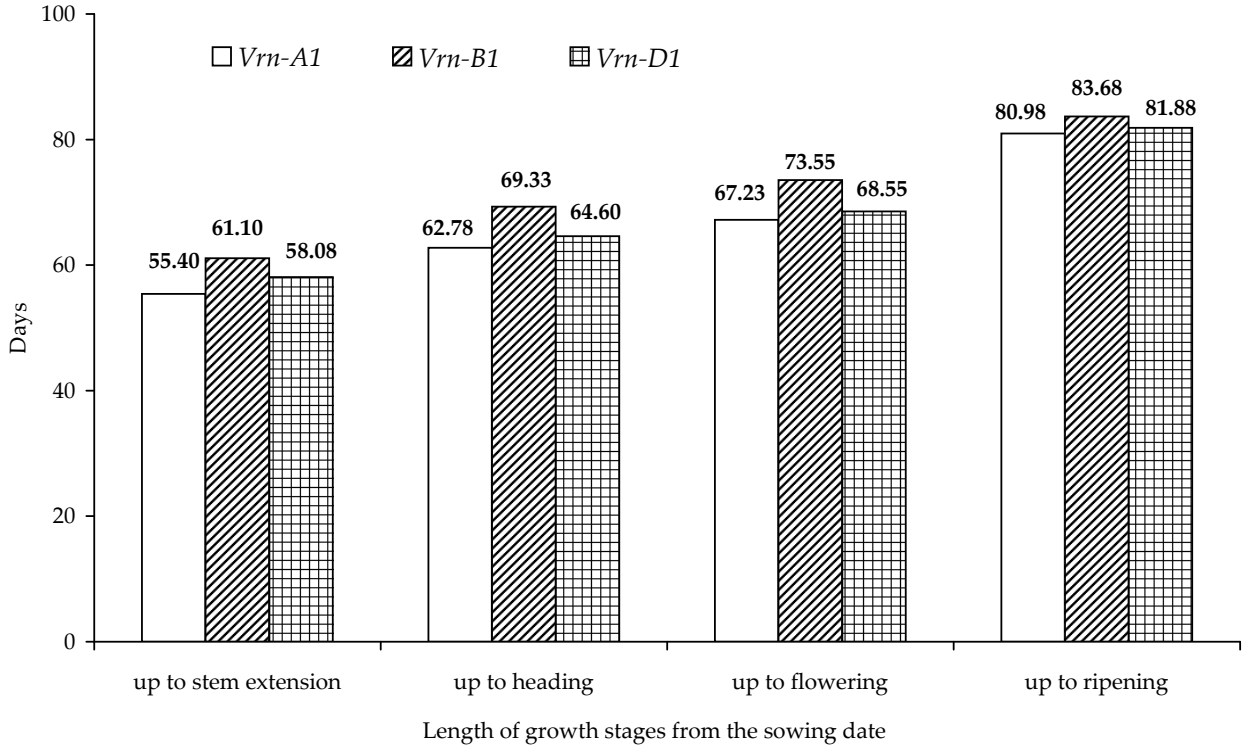

Figure 2. The effect of dominant genes *Vrn* on combined growth stages

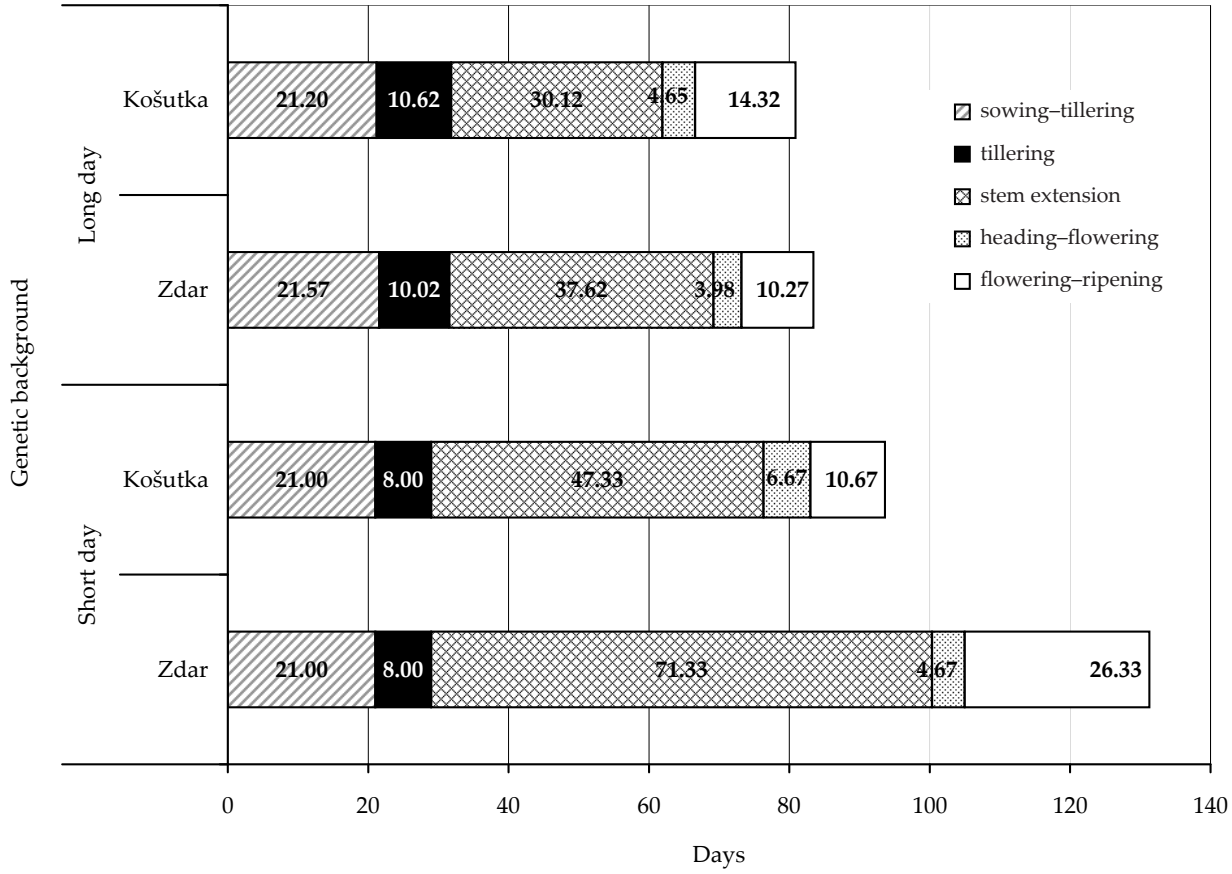

Figure 3. The effect of genetic background at different day length on growth stages

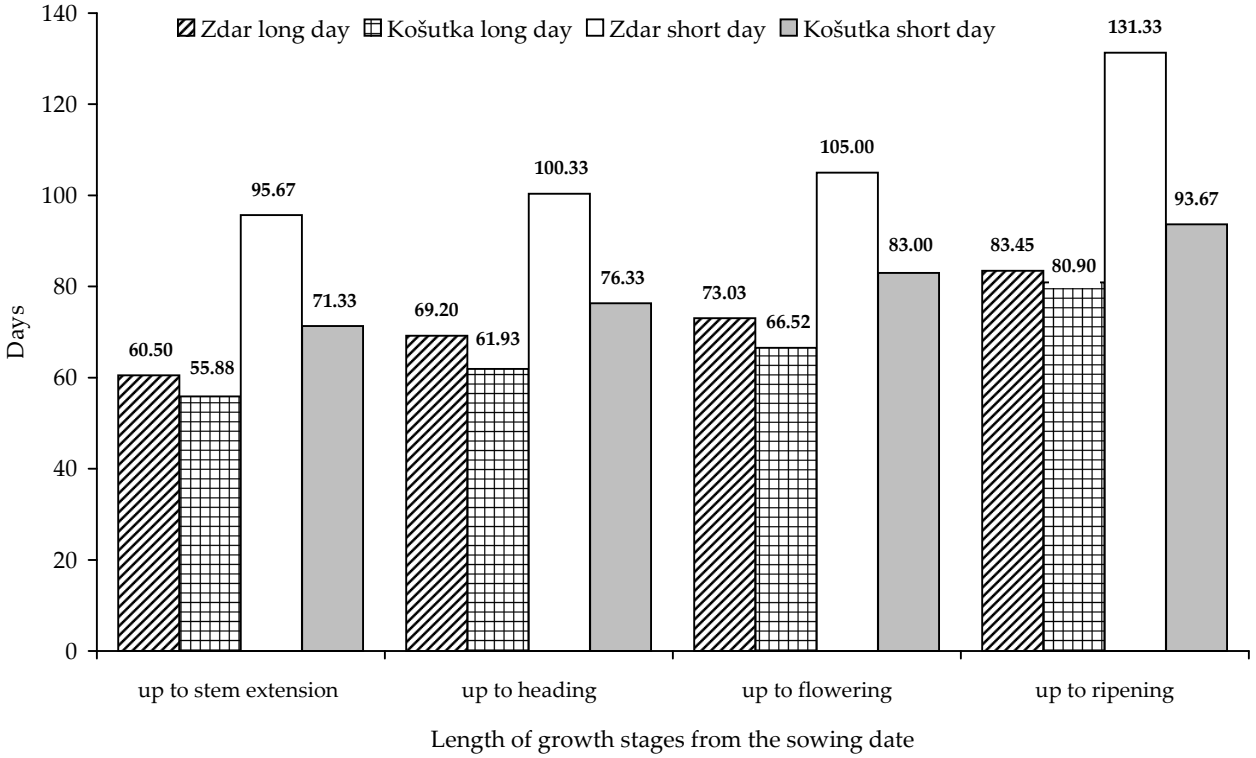

Figure 4. The effect of genetic background at different day length on growth stages

The effect of photoperiod on growth stages of the lines with different photoperiod sensitivity was analysed by comparing the growth stages of the materials grown under a 10-hour photoperiod. The ten-hour photoperiod was stopped in the middle of July to obtain heading in lines with the sensitive background of Zdar. After the concurrent start, considerable differences were observed in the development of the lines after the elongation growth stage was achieved. Interestingly, the length of the stage from heading to flowering was not different between the backgrounds of Zdar and Košutka (Figures 3 and 4).

The main treatment of the experiment related to ten subsequent sowing dates at weekly intervals. They significantly affected the elongation growth stage and the stages from flowering to ripening. The length of growth stages obviously results from the co-operation between genetic (*Vrn* loci, background, *Ppd* loci) and environmental factors (sowing dates), which was expected regarding the large range of the latter ones. Interaction between chromosomes and genetic background shows how much the chromosomes carrying the *Vrn* loci and genetic background participate in the expression of the evaluated traits. The length of growth stages is possibly influenced by the co-operative action of *Vrn* loci and photoperiod sensitivity.

The influence of individual *Vrn* loci on the growth stages under different environmental conditions (various sowing dates) was confirmed by a low incidence of significant interactions between *Vrn* loci and sowing dates. We can suppose an independent action of the genetic factors under the environmental conditions.

Conclusions

The duration of growth stages was distinctly affected by the substituted chromosomes, and thence by the *Vrn* loci present, besides the influence of sowing dates and genetic background.

The *Vrn-A1* locus most efficiently and *Vrn-B1* least efficiently reduced the growth stages. The difference of 6.5 days in the length of the period from sowing to heading or flowering was found between the effects of *Vrn-A1* and *Vrn-B1*; the lines carrying *Vrn-A1* were earlier. The effect of *Vrn-D1* was intermediary, nearer to *Vrn-A1* than to *Vrn-B1*.

The genetic backgrounds of cultivars Zdar and Košutka differ markedly in their photoperiod re-

sponse, Zdar being sensitive while Košutka is insensitive to photoperiod.

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Souhrn

Pánková K., Košner J. (2004): **Chromosomové substituce s dominantními lokusy *Vrn-1* a jejich účinek na vývojové fáze pšenice**. Czech J. Genet. Plant Breed., **40**: 37–44.

Soubor šesti substitučních linií se změnou ozimého růstového typu v jarní byl získán substitucemi chromosomů páté homoeologické skupiny, nesoucích dominantní geny *Vrn-A1*, *Vrn-B1* a *Vrn-D1*, do genetických pozadí ozimých odrůd Zdar (citlivý k fotoperiodě) a Košutka (necitlivá k fotoperiodě), a tedy nahrazením přítomných

recesivních alel *vrn-A1*, *vrn-B1*, *vrn-D1* dominantními alelami. Byl studován vliv substituovaných chromosomů nesoucích jednotlivé lokusy *Vrn* na růstové fáze pšenice. Ověřené donorové odrůdy dominantních lokusů jsou: Zlatka (*Vrn-A1*, chromosom 5A), Česká Přesívka (*Vrn-B1*, chromosom 5B) a Chinese Spring (*Vrn-D1*, chromosom 5D). Substituční linie byly vysety do pole v týdenních intervalech v 10 termínech a jejich vývojové stupně byly zaznamenávány pro zjištění účinku substitucí. Tyto linie byly též paralelně pěstovány v krátkodenních podmínkách (10 hodin) pro vyhodnocení jejich fotoperiodické citlivosti. Analýza získaných výsledků potvrdila výrazný vliv chromosomu 5A nesoucího lokus *Vrn-A1* na průběh růstových fází vedle vlivu data výsevu a genetického pozadí. Největší zkrácení růstových fází bylo zjištěno u linií se substitucemi chromosomu 5A (*Vrn-A1)*, zatímco nejmenší redukce nastala u linií se substituovaným chromosomem 5B (*Vrn-B1)*. Největší dosažený rozdíl v době do metání, 6,5 dne, nastal mezi liniemi s chromosomovými substitucemi nesoucími lokusy *Vrn-A1* a *Vrn-B1*. Účinek substitucí s *Vrn-D1* byl intermediální.

Klíčová slova: *Triticum aestivum*; pšenice; *Vrn*; růstový typ; růstové fáze

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