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Length of Prematurity Period in Wheat Cultivars Determines Maximum Cereal Aphid Abundance

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Abstract

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Maximum aphid numbers on wheat are positively related to the length of the period elapsed from immigration to the population peak. We predicted that maximum abundances on late maturing cultivars would be greater than on early ones. This was tested using 8 spring wheat cultivars that differed in the length of time to senescence. In a 4-year experiment, numbers of aphids were checked at weekly intervals. Maximum abundances on late-maturing cultivars were significantly greater than those on early cultivars. However, the length of the vegetation period affected maximum abundances less than did the annual variation in aphid abundance. Genetic disposition for early ripening thus tends to decrease aphid numbers, but manipulation of this character is unlikely to become an important source of aphid resistance.

Keywords: flowering time; *Metopolophium dirhodum*; population; *Rhopalosiphum padi*; *Sitobion avenae*; spring wheat

Aphids are important pests of cereals, and their biology has been studied with corresponding effort (Vickerman & Wratten 1979; Dixon 1987; Dedryver *et al.* 2010). The virus transmission causes a significant damage. In addition, aphids sucking on leaves and ears decrease seed mass and may cause significant damage in years when aphids are abundant (Niehoff & Stäblein 1998; Larsson 2005). Plants are damaged by the removal of assimilates transported to and within ears. The loss of grain yield is proportionate to the numbers of aphids and the length of their stay on the crop (Kieckhefer *et al*. 1995). These parameters of aphid population development depend on both aphid biology and crop development.

The dominant aphid species in Central Europe – *Metopolophium dirhodum* (Walker) (MD), *Rhopalosiphum padi* (L.) (RP), and *Sitobion avenae* (F.) (SA) – are all holocyclic (reproducing by a series of parthenogenetic generations alternating with a single sexually reproducing generation) and are either heteroecious (occupying herbaceous and woody hosts at different stages of the life cycle – MD, RP) or monoecious (living on herbaceous hosts throughout the season – SA) (Blackman & Eastop 1984). In spring, after hatching from eggs and passing a few generations on their winter hosts, *Rosa* spp. (MD), *Prunus* spp. (RP), and Gramineae (SA), winged migrants, leave the winter hosts and settle on cereal crops. All these species are typical "flush-feeders" (White 2015) that benefit from feeding on young, vigorous plants.

In cereal stands, aphids produce several generations. Their populations grow exponentially and, after attaining maximum abundance, quickly recede (Honek 1994; Honek & Martinkova 1999). The time of population collapse usually correlates with the onset of the host plant's "maturation", approximately growth stage GS80–GS85 in winter wheat (Tottman & Broad 1987). However, aphid populations colonising late-sown wheat (Honek & Martinkova 2004a)

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and maize crops (Honek 1994) also recede from host plants in early July, although the host plants are still physiologically young and convenient for continuing aphid breeding. In this case, the main causes of aphid mortality on young plants are mycoses (Honek & Martinkova 2004a). The maximum number of aphids on a crop stand (population peak) is determined by three population parameters: (*i*) initial number of immigrants, (*ii*) rate of population increase, which is determined by female developmental time and fecundity, and (*iii*) duration of the period of population increase, which is the time elapsed from immigration to the population peak (Honek 1991c; Honek *et al*. 2006). The effects of immigrant numbers (Basky & Harrington 2000; Klueken et al. 2009) and of factors determining the population growth rate, host plant quality (Honek 1991b; Honek & Martinkova 2004b), temperature (Dean 1974; Brabec *et al*. 2014), aphid reproduction rate (Simon *et al*. 1991; Sengonca *et al*. 1994), and presence of natural enemies (Leslie *et a*l. 2009; Kerzicnik *et al*. 2010) are well studied. In contrast, factors that determine the duration of the period of aphid population increase have not been sufficiently addressed. The length of this period increases when immigration occurs earlier and the population peak is postponed. In Central Europe, aphid migration to cereals takes place in May. Immigration is timed based on the thermal response of overwintering aphid populations and depends on winter and spring weather (Klueken *et al*. 2009; Brabec *et al*. 2014). After immigration, aphids continue to benefit from host plants as long as photosynthetic products are translocated. Their populations grow until peak density is attained. The peak is followed by a quick population collapse that results from decreasing natality, increasing mortality, and the massive production and emigration of alatae (Vereijken 1979; Ba-Angood & Stewart 1980). Extending the vegetation period of the host plant through a delay of maturation extends the period available for aphid population growth and will likely increase the maximum aphid numbers (Honek & Martinkova 2004b).

Seasonal development of host-plant and aphid populations has been tuned through their long evolutionary coexistence. However, unlike wild plants, crops have been subjected to intensive selection on morphological and physiological traits that modified their relationship to phytophagous insects (Chen *et al*. 2015). In wheat, this genetic manipulation also affected the developmental timing, resulting in variations in flowering time and the length of the period to maturation and senescence. As a side effect, variation in these characters influences maximum aphid abundances. In cereals, one of the manipulated traits is time to flowering (period from growth stage GS10 to GS65) which is correlated with time to crop maturation, a period extended to approximately GS80–GS85 (stages critical for aphid population collapse), henceforth referred to as the "vegetation period". Genetic factors that delay flowering also lengthen the vegetation period. A series of photoperiod and vernalization genes are the main components regulating genetic control of flowering time. The homoeoloci *Ppd-A1*, *Ppd-B1,* and *Ppd-D1* are responsible for most of the photoperiod response and are located on the short arms of chromosomes 2A, 2B, and 2D, respectively (Welsh *et al.* 1973; Law *et al*. 1978; Mohler *et al*. 2004). The vernalisation response is mostly controlled by the homoeoloci *Vrn-A1*, *Vrn-B1,* and *Vrn-D1*, which have been mapped to the long arms of chromosomes 5A, 5B, and 5D, respectively (Sarma *et al*. 1998; Leonova *et al*. 2003; Shindo *et al*. 2003). Breeding for decreased/increased flowering time changes the length of the vegetation period (Cockram *et al*. 2007; Milec *et al*. 2013).

The positive effect of extended vegetation period on aphid abundance was documented in winter wheat using stands whose development rate was manipulated by agricultural practices (Honek 1987; Honek & Martinkova 1999). However, there is little information concerning the effect of genetic variation in the length of vegetation period on maximum aphid abundance. This is probably because studies of aphid population development have mostly been performed on winter wheat, for which genetic differences in the length of vegetation period are small. For instance, winter wheat cultivars recommended for use in the Czech Republic differ in length of the vegetation period by ≤ 7 days (UKZUZ 2015). By contrast, the length of the vegetation period in spring wheat cultivars is more variable; moreover, the genetics of a number of cultivars, including those discussed in this study, has been well studied.

In this study, we selected spring wheat cultivars with differing lengths of the time to flowering and tested a hypothesis predicting a positive relationship between the time length of a cultivar to flowering (a good proxy of the length of vegetation period; Pánková *et al*. 2008) and the maximum abundance of the aphid population. This means that late-flowering cultivars would support greater maximum aphid populations than early-flowering ones.

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MATERIAL AND METHODS

Cultivars. We selected four early-flowering (Kaerntner Frueher, Mané Nick, Crespon, Artur Nick) and four late-flowering (Paragon, Trappe, Almansor, Česká přesívka) spring wheat cultivars. The flowering date of each cultivar was recorded when the ear on the leading tiller had half emerged (Pánková *et al*. 2008). Flowering time means the period elapsed from the penetration of the first leaf through the coleoptile (GS10 of the Decimal Code system for measuring wheat growth; Tottman & Broad 1987) to the date of flowering. Flowering time is a convenient proxy for the length of the period to crop maturation (vegetation period), during which the cultivar is suitable for aphid growth. In the eight cultivars included in this study, flowering time differed by nearly one month (Table 1).

DNA extraction and PCR. The present study updates earlier data on the distribution of vernalization genes in selected cultivars (Milec *et al*. 2013). DNA was extracted from five different fresh wheat leaves from individuals of each variety using a modified cetyltrimethylammonium bromide method (Doyle & Doyle 1987). Polymerase chain reaction (PCR) was performed in a DNA Engine® PTC-200 cycler (Bio-Rad, Hercules, USA) in a total volume of 11 µl. The reaction mixture contained 1.5 µl of 10 × PCR buffer containing $MgCl_2$, 1.5 µl of 2 mM dNTP mixture, 1.5 µl of 2 µM primers (total volume for each primer), 0.07 µl of Taq DNA polymerase (5 U/µl) (all Roche Diagnostics GmbH, Mannheim, Germany), and 100–150 ng of template DNA. For the analysis of *Ppd-A1*, *Ppd-D1*, and the presence of the *Vrn-A1, Vrn-B1,* and *Vrn-D1* alleles, protocols from Fu *et al*. (2005), Beales *et al*. (2007), Milec *et al*. (2012), and Nishida *et al*. (2012) were used. The alleles were differentiated according to fragment length and dominant markers. The obtained PCR products were then separated on 2.0% agarose gels, stained with ethidium bromide and visualised under ultraviolet light.

Field experiments. The experiments were performed in 2011–2014 in a field belonging to the Crop Research Institute at Prague-Ruzyne (50.09 N, 14.30 E, altitude 340 m a.s.l.), using solitary plants, which are known to support greater aphid populations than plants in dense stands (Honek 1991a, d). Spring cultivars were sown on an experimental field using agricultural practices modified to satisfy the standards of organic agriculture. The preceding crop was white mustard, which was sown in mid-July and ploughed down in September as green manure. The following spring, the experimental plot was harrowed and rolled before sowing. No fertilizers or pesticides were used, and weeds were removed mechanically. A net (3 × 3 cm, nylon fibre diameter 0.3 mm, green) was stretched over a 1.5 m high cage construction above the experimental plot to prevent vertebrate (pheasant, hare) grazing while permitting access to invertebrates.

The experimental plants were sown on April 1, 2011 and March 26 and 23, 2012 (two sowing dates with three blocks each; results from 2012 were pooled because there were no differences in aphid abundance between plants of the two sowing dates), April 17, 2013 (two blocks used for analysis, one block destroyed by hamsters), and April 16, 2014. The experimental design was identical for all sowing dates. Each replicate was a row of 30 plants (120 cm long, 4 cm between plants), and each block was eight rows (one row of each of eight cultivars; row spacing was 60 cm), with 3 blocks per sowing date. The cultivar position in the rows within each block was randomised. This means that for each sowing date, each of the 8 cultivars was sown in 3 replicates, i.e.

Table 1. List of cultivars used in this study, showing cv name and acronym, flowering time (FT) (number of days from GS10 to GS65 established in preliminary field experiments), and the presence of *Vrn* and *Ppd* genes in the genetic constitution of individual cvs Dominant alleles are designated by capitals, and recessive alleles are designated by small initial letters

Cultivar		FT	*vrn-A1*	*vrn-B1*	*vrn-D1*	*Ppd-A1*	*Ppd-D1*
Kaerntner Frueher	KAER	57.8	*Vrn-A1a*	*Vrn-B1c*	*vrn-D1*	*Ppd-A1b*	*Ppd-D1b*
Mané Nick	MANI	59.7	*Vrn-A1a*	*vrn-B1*	*Vrn-D1*	*Ppd-A1b*	*Ppd-D1a*
Crespon	CRES	61.4	*Vrn-A1a*	*vrn-B1*	*vrn-D1*	*Ppd-A1b*	*Ppd-D1a*
Artur Nick	ARNI	62.1	*Vrn-A1a*	*vrn-B1*	*vrn-D1*	*Ppd-A1b*	*Ppd-D1a*
Paragon	PARA	68.9	*Vrn-A1a*	*Vrn-B1c*	*vrn-D1*	*Ppd-A1b*	*Ppd-D1b*
Trappe	TRAP	70.4	*Vrn-A1a*	*Vrn-B1a*	*vrn-D1*	*Ppd-A1b*	*Ppd-D1b*
Almansor	ALMA	71.5	*vrn-A1*	*Vrn-B1a*	*vrn-D1*	*Ppd-A1b*	*Ppd-D1a*
Česká přesívka	CEPR	84.2	*vrn-A1*	*Vrn-B1a*	*vrn-D1*	*Ppd-A1b*	*Ppd-D1b*

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n = 24 replicates. The total n = 24 [2011] + 48 [2012, two sowing dates] + 16 [2013, one block deleted] + 24 [2014] = 112 replicates available for analysis.

Aphid counts. Aphid species (MD, RP, and SA) were counted separately on leaves and ears. Counts started in mid-May, 5–6 weeks before aphids attained maximum abundance. Each year, weekly aphid counts in spring wheat were performed on 30 fertile tillers per replicate (or the tallest tillers before earing) and continued until there were no more aphids present on the crop. Aphid numbers per tiller were calculated as a sum of the mean number on leaves and that on ears. Data were recorded as aphids per tiller within each replicate (row), and mean weekly densities were calculated by averaging across replicates of particular cultivars. The date when the average aphid abundance (a mean calculated of aphid abundances on all individual cultivars) was the highest was set as the "aphid population peak".

Data analysis. Differences among cultivars were tested using results of the date of aphid population peak when average aphid abundance (a mean calculated from aphid abundances on all individual cultivars) was the highest. Annual variation in aphid numbers was tested using data on the peak abundance for individual replicates and years, using two-way ANOVA with peak abundance as the response variable and year and cultivar as factors. For testing the effect of cultivar specific flowering time on aphid abundance at the population peak, the large effect of annual variation was balanced using standardisation. Data for individual replicates were standardised within years as:

$$x_s = (x_o - x_a)/s_x$$

where: x_s – standardised value of mean aphid abundance in a particular replicate; x_o – experimental value of aphid abundance in a particular replicate; x_a – average; s_x – standard deviation of the aphid abundance values on all replicates together (Hendl 2009)

Standardisation compensated for the important annual variation in aphid abundance (Wetzel 2004; Brabec *et al.* 2014), which would conceal cultivar differences. The standardized values (x_s) were regressed on flowering time as a proxy for the cultivar-specific length of vegetation period, using second-order polynomial regression $y = a + bx_s + cx_s^2$. The differences in x_s of early cultivars and late cultivars were tested using the Mann-Whitney (MW) test. The arithmetic means ± standard error of the means are given throughout the text. Calculations were performed using SigmaStat® (Systat Software 2006).

RESULTS

In individual years, the peak abundance of aphids on spring cultivars occurred between June 30th (Julian day 182) and July 8th (Julian day 190) with an average on Julian day 186.8 ± 1.80.

Individual aphid species contributed unevenly to aphid population (Table 2). Within the total aphid population, the dominant species MD represented an average of 60.4 ± 4.23%, followed by SA (30.3 ± 3.96%) and RP (9.4 ± 3.03%). MD inhabited only leaves and represented 76.1 ± 4.28% of the aphid population on leaves, followed by SA (14.7 ±3 .06%) and RP (9.3 ± 3.35%). On ears, the aphid population consisted only of SA (86.3 ± 5.10%) and RP (13.7 ± 5.10%). All differences were significant at $P_{MW} < 0.001$.

The variation in maximum aphid abundances was considerable (Table 2), and it was more important among years (two-way ANOVA: $F_{3,80} = 16.76$, $P < 0.001$) than among cultivars ($F_{7,80} = 3.026$, $P = 0.005$). There was a significant year × cultivar interaction ($F_{21,80} = 2.22$, $P = 0.006$) caused by the large annual variation in aphid abundance on the early cultivar Artur Nick and the late cultivars Paragon, Trappe, and Almansor.

Compensating for annual differences using standardisation of data resulted in a significant ($df = 111$, $R = 0.3885$, $P < 0.001$) non-linear regression of maximum aphid abundance on the length of flowering time (Figure 1). While maximum aphid abundances were lower (3.9 ± 0.80 aphids/tiller) on the early-flowering cvs Kaerntner Frueher, Mané Nick, Crespon, and Artur Nick (mean flowering time 60.3 ± 0.96 days), three late-flowering cvs Paragon, Trappe, Almansor (mean flowering time 70.3 ± 0.75 days) hosted significantly (U = 726.500, $P_{MW} = 0.004$) greater aphid populations (5.5 ± 1.22 aphids/tiller). However, cv. Česká přesívka, with a very long flowering time, hosted low aphid populations (2.7 ± 0.36 aphids/tiller).

DISCUSSION

The effect of crop seasonality (length of the vegetation period) on the development of aphid populations became apparent from this study. The work conclusively demonstrated a significant association between variation in the length of the vegetation period (flowering time) and peak aphid abundance. The results were consistent with the hypothesis predicting a positive relationship between the vegetation period of a cultivar (flowering time) and the abundance of aphid populations on that

Table 2. Average maximum abundance (± SE) of individual aphid species, *Metopolophium dirhodum* (MD), *Sitobion avenae* (SA), *Rhopalosiphum padi* (RP), and total numbers on leaves, ears, and whole tillers. For each year and cultivar, the average (± SE) number of aphids was calculated using two (2013), three (2011, 2014) or six (2012) replicates, and each replicate represented data from 30 tillers

Year	Cultivar	Leaf				Ear			Total
		MD	SA	RP	total	SA	RP	total	
2011	Kaerntner Frueher	0.4 ± 0.44	0.0 ± 0.03	4.1 ± 3.00	4.6 ± 2.88	0.9 ± 0.38	0.0 ± 0.03	1.0 ± 0.38	5.5 ± 2.50
	Mané Nick	1.4 ± 0.16	1.0 ± 0.70	1.0 ± 0.51	3.4 ± 1.24	0.6 ± 0.54	0.0 ± 0.00	0.6 ± 0.54	4.0 ± 1.45
	Crespon	1.0 ± 0.85	3.4 ± 2.19	2.8 ± 2.76	7.3 ± 3.79	4.0 ± 1.53	0.1 ± 0.06	4.0 ± 1.54	11.3 ± 3.70
	Artur Nick	6.4 ± 2.21	1.0 ± 0.59	0.1 ± 0.01	7.4 ± 1.98	2.1 ± 0.67	0.1 ± 0.09	2.2 ± 0.74	9.6 ± 1.67
	Paragon	3.9 ± 0.63	2.5 ± 1.78	0.4 ± 0.18	6.8 ± 1.58	2.2 ± 0.52	0.0 ± 0.00	2.2 ± 0.52	8.9 ± 2.04
	Trappe	1.3 ± 0.76	0.4 ± 0.16	0.0 ± 0.02	1.8 ± 0.65	0.5 ± 0.34	0.0 ± 0.00	0.5 ± 0.34	2.2 ± 0.67
	Almansor	3.6 ± 1.79	5.4 ± 3.84	0.1 ± 0.04	9.0 ± 5.60	7.3 ± 3.50	0.0 ± 0.00	7.3 ± 3.50	16.4 ± 7.59
	Česká přesívka	1.7 ± 0.73	1.0 ± 0.58	0.1 ± 0.14	2.8 ± 1.28	0.5 ± 0.32	0.0 ± 0.00	0.5 ± 0.32	3.3 ± 1.13
2012	Kaerntner Frueher	1.0 ± 0.31	0.0 ± 0.00	0.0 ± 0.02	1.0 ± 0.30	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	1.0 ± 0.30
	Mané Nick	0.4 ± 0.26	0.0 ± 0.00	0.3 ± 0.12	0.7 ± 0.32	0.0 ± 0.01	0.1 ± 0.05	0.1 ± 0.04	0.8 ± 0.32
	Crespon	0.8 ± 0.30	0.0 ± 0.00	0.1 ± 0.04	0.9 ± 0.31	0.0 ± 0.04	0.0 ± 0.00	0.0 ± 0.04	0.9 ± 0.32
	Artur Nick	0.3 ± 0.14	0.0 ± 0.00	0.0 ± 0.02	0.4 ± 0.13	0.2 ± 0.10	0.1 ± 0.04	0.2 ± 0.10	0.6 ± 0.20
	Paragon	3.0 ± 0.75	0.2 ± 0.18	0.0 ± 0.02	3.2 ± 0.73	0.1 ± 0.05	0.1 ± 0.05	0.1 ± 0.06	3.3 ± 0.71
	Trappe	1.1 ± 0.34	0.0 ± 0.00	0.6 ± 0.30	1.7 ± 0.48	0.0 ± 0.01	0.2 ± 0.17	0.2 ± 0.17	1.9 ± 0.39
	Almansor	3.8 ± 1.55	0.0 ± 0.01	0.9 ± 0.54	4.8 ± 2.05	0.1 ± 0.03	0.9 ± 0.90	1.0 ± 0.89	5.8 ± 1.85
	České přesívka	1.5 ± 0.26	0.0 ± 0.03	0.1 ± 0.07	1.7 ± 0.32	0.1 ± 0.04	0.0 ± 0.01	0.1 ± 0.04	1.7 ± 0.35
2013	Kaerntner Frueher	1.6 ± 0.67	0.0 ± 0.03	0.0 ± 0.00	1.6 ± 0.70	0.4 ± 0.18	0.0 ± 0.00	0.4 ± 0.18	2.0 ± 0.87
	Mané Nick	3.5 ± 0.95	0.5 ± 0.37	0.0 ± 0.00	3.9 ± 0.58	1.2 ± 0.74	0.0 ± 0.00	1.2 ± 0.74	5.1 ± 0.16
	Crespon	4.7 ± 1.48	0.2 ± 0.04	0.0 ± 0.00	4.8 ± 1.52	0.3 ± 0.20	0.0 ± 0.02	0.3 ± 0.22	5.1 ± 1.74
	Artur Nick	0.4 ± 0.39	0.0 ± 0.00	0.0 ± 0.00	0.4 ± 0.39	0.2 ± 0.17	0.0 ± 0.00	0.2 ± 0.17	0.6 ± 0.56
	Paragon	2.6 ± 0.55	0.2 ± 0.08	0.0 ± 0.00	2.8 ± 0.64	0.0 ± 0.05	0.0 ± 0.00	0.0 ± 0.05	2.9 ± 0.59
	Trappe	2.9 ± 1.68	0.0 ± 0.02	0.0 ± 0.00	3.0 ± 1.69	0.9 ± 0.35	0.0 ± 0.00	0.9 ± 0.35	3.8 ± 1.34
	Almansor	2.7 ± 2.72	0.0 ± 0.03	0.0 ± 0.00	2.8 ± 2.69	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	2.8 ± 2.69
	Česká přesívka	0.3 ± 0.01	0.2 ± 0.17	0.0 ± 0.00	0.4 ± 0.16	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.4 ± 0.16
2014	Kaerntner Frueher	1.2 ± 0.47	0.0 ± 0.04	0.1 ± 0.10	1.3 ± 0.40	0.5 ± 0.23	0.0 ± 0.01	0.5 ± 0.24	1.8 ± 0.62
	Mané Nick	1.7 ± 0.64	0.3 ± 0.29	0.0 ± 0.02	2.0 ± 0.94	1.5 ± 0.42	0.2 ± 0.12	1.7 ± 0.53	3.7 ± 0.74
	Crespon	1.5 ± 0.92	0.1 ± 0.08	0.0 ± 0.00	1.6 ± 1.00	3.4 ± 0.74	0.0 ± 0.00	3.4 ± 0.74	5.1 ± 1.69
	Artur Nick	3.3 ± 1.28	0.1 ± 0.04	0.0 ± 0.00	3.4 ± 1.30	2.5 ± 0.10	0.0 ± 0.00	2.5 ± 0.10	5.9 ± 1.38
	Paragon	3.6 ± 0.54	0.5 ± 0.17	0.0 ± 0.00	4.1 ± 0.71	1.7 ± 1.02	0.0 ± 0.04	1.7 ± 1.06	5.8 ± 1.70
	Trappe	3.9 ± 1.60	2.5 ± 1.65	0.0 ± 0.00	6.4 ± 3.20	3.0 ± 1.23	0.0 ± 0.00	3.0 ± 1.23	9.4 ± 4.35
	Almansor	1.5 ± 0.59	0.6 ± 0.43	0.0 ± 0.00	2.1 ± 1.02	1.3 ± 0.34	0.0 ± 0.03	1.3 ± 0.34	3.4 ± 1.31
	Česká přesívka	1.0 ± 0.51	0.7 ± 0.26	0.0 ± 0.00	1.7 ± 0.37	0.1 ± 0.15	0.0 ± 0.00	0.1 ± 0.15	1.8 ± 0.49

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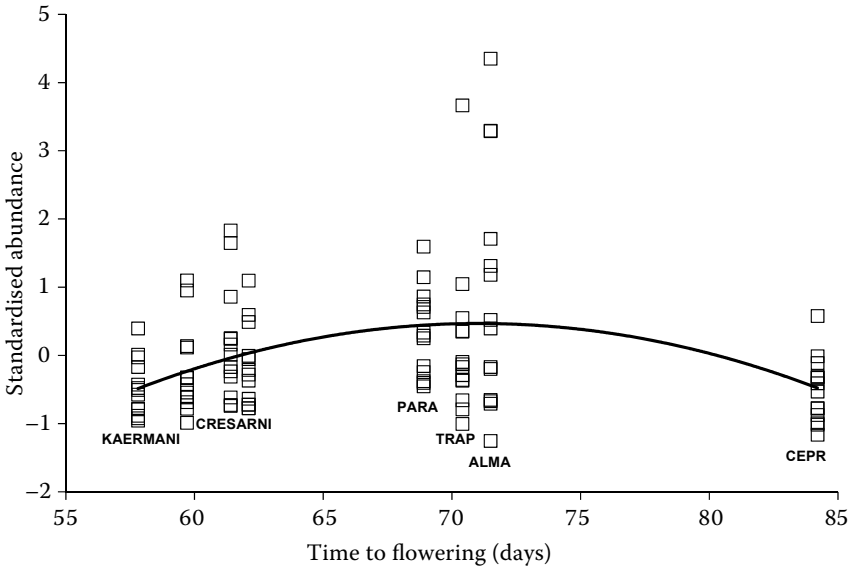

Figure 1. Standardised abundance of aphids (pooled number for all species tiller-1) in relation to flowering time of wheat cultivars (a = −27.06, b = 0.771, c = −0.0055, R^2 = 0.1509, P < 0.001). Each replicate is represented by an individual symbol (for acronyms see Table 1)

cultivar. Maximum aphid abundance was significantly greater in late-flowering cultivars (Paragon, Trappe, Almansor) than in early-flowering cultivars (Kaerntner Frueher, Mané Nick, Crespon, Arthur Nick). Aphid immigration on individual cultivars was synchronous, and then a 10-day difference in vegetation period (flowering time) was sufficient to cause a significant variation in maximum aphid numbers.

In our experiments, aphid decline always occurred during the week after the population peak, even when late cultivars still appeared convenient for aphid breeding. This decline was connected with an interesting fact: the positive effect of the length of the vegetation period on peak aphid numbers was not linear. In the very late cv. Česká přesívka, maximum abundances were consistently low. The development of cv. Česká přesívka was so delayed that the earing and flowering stages came as late as after the aphid retreat from the crop stand. The spontaneous retreat of aphids from still physiologically favourable cereal crops occurs in early July (Honek & Martinkova 2004a), probably largely because of spreading diseases, increased production and the emigration of alatae. Factors other than host-plant quality may contribute to alatae production, possibly including photoperiod, the effect of which on the production of alate virginoparae has sometimes been reported in different aphid species (MacGillivray & Anderson 1964; Yasue & Kawada 1969) but is not recognised as a factor of alary polymorphism in cereal aphid virginoparae. A similar collapse of cereal aphid populations occurs in early summer on maize crops that are still far from senescence (Honek 1994; Honek *et al.* 1998).

Early flowering and a short vegetation period (time necessary to reach growth stage GS80) slightly decreased maximum aphid abundances compared to late flowering, which is associated with a long vegetation period. The genetic constitution of spring cultivars definitely influences crop seasonality, but details of the genetic factors that determine differences in flowering time and the length of the vegetation period are not yet completely clear. Information on the main factors affecting these traits, specifically alleles of the *Vrn* and *Ppd* genes (Table 1), may provide potentially useful information for wheat breeding for pest resistance. Late flowering confers some risk of increasing aphid abundance on cereals. However, this risk is apparently small and probably not of practical importance under the usual conditions of Central Europe, as in our experiment. This is mainly because significant differences manifested as late as in early July and by that time aphid populations already began to decline spontaneously. The significance of variation in the length of the vegetation period for determining maximum aphid numbers remains to be studied under different agricultural practices (fertilisation, sowing date) and climates, where its effect may be greater than in our experiments and thus important from the perspective of crop protection.

References

Ba-Angood S.A., Stewart R.K. (1980): Occurrence, development, and distribution of cereal aphids on early and late cultivars of wheat, barley, and oats in southhwestern Quebec. Canadian Entomologist, 112: 615–620.

doi: 10.17221/3/2016-PPS

Basky Z., Harrington R. (2000): Cereal aphid flight activity in Hungary and England compared by suction traps. Anzeiger für Schädlingskunde Pflanzenschutz Umweltschutz, 73: 70–74.

Beales J., Turner A., Griffiths S., Snape J.W., Laurie D.A. (2007): A pseudo-response regulator is misexpressed in the photoperiod insensitive *Ppd-D1a* mutant of wheat (*Triticum aestivum* L.). Theoretical and Applied Genetics, 115: 721–733.

Blackman R.L., Eastop V.F. (1984): Aphids on the World's Crops. Chichester, NewYork, Brisbane, Toronto, Singapore, John Wiley and Sons.

Brabec M., Honěk A., Pekár S., Martinková Z. (2014): Population dynamics of aphids on cereals: digging in the time-series data to reveal population regulation caused by temperature. PLoS ONE 9: e106228. doi: 10.1371/journal.pone.0106228

Chen Y.H., Gols R., Benrey B. (2015): Crop domestication and its impact on naturally selected trophic interactions. Annual Review of Entomology, 60: 35–58.

Cockram J., Jones H., Leigh F.J., O'Sullivan D., Powell W., Laurie D.A., Greenland A.J. (2007): Control of flowering time in temperate cereals: genes, domestication, and sustainable productivity. Journal of Experimental Botany, 58: 1231–1244.

Dean G.J. (1974): Effect of temperature on the cereal aphids-*Metopolophium dirhodum* (Wlk.), *Rhopalosiphum padi* (L.) and *Macrosiphum avenae* (F.) (Hem., Aphididae). Bulletin of Entomological Research, 63: 401–409.

Dedryver C.A., Le Ralec A., Fabre F. (2010): The conflicting relationships between aphids and men: a review of aphid damage and control strategies. Comptes Rendus Biologies, 333: 539–553.

Dixon A.F.G. (1987): Cereal aphids as an applied problem. Agricultural Zoology Review, 2: 1–57.

Doyle J.J., Doyle J.L. (1987): A rapid DNA isolation procedure for small quantities of fresh leave tissue. Phytochemical Bulletin, 19: 11–15.

Fu D.L., Szucs P., Yan L.L., Helguera M., Skinner J.S., von Zitzewitz J., Hayes P.M., Dubcovsky J. (2005): Large deletions within the first intron in VRN-1 are associated with spring growth habit in barley and wheat. Molecular Genetics and Genomics, 273: 54–65.

Hendl J. (2009): Přehled statistických metod: analýza a metaanalýza. Praha, Portal.

Honek A. (1987): Effect of plant quality and microclimate on population growth and maximum abundances of cereal aphids, *Metopolophium dirhodum* (Walker) and *Sitobion avenae* (F.) (Hom., Aphididae). Zeitschrift für Angewandte Entomologie, 104: 304–314.

Honek A. (1991a): Environment stress, plant quality and abundance of cereal aphids (Hom., Aphididae) on winter wheat. Journal of Applied Entomology, 112: 65–70.

Honek A. (1991b): Nitrogen fertilization and abundance of the cereal aphids *Metopolophium dirhodum* and *Sitobion avenae* (Homoptera, Aphididae). Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz, 98: 655–660.

Honek A. (1991c): Factors determining the peak abundance of *Metopolophium dirhodum* (Homoptera, Aphididae) on cereals. Bulletin of Entomological Research, 81: 57–64.

Honek A. (1991d): Dry mass allocation in cereal plants and distribution of *Metopolophium dirhodum* and *Sitobion avenae* (Homoptera: Aphididae). Acta Entomologica Bohemoslovaca, 88: 103–109.

Honek A. (1994): The effect of plant quality on the abundance of *Metopolophium dirhodum* (Homoptera: Aphididae) on maize. European Journal of Entomology, 91: 227–236.

Honek A., Martinkova Z. (1999): Host-plant mediated influences on population development of *Sitobion avenae* (Sternorrhyncha: Aphididae). European Journal of Entomology, 96: 135–141.

Honek A., Martinkova Z. (2004a): Host plant age and population development of a cereal aphid, *Metopolophium dirhodum* (Hemiptera: Aphididae). Bulletin of Entomological Research, 94: 19–26.

Honek A., Martinkova Z. (2004b): The effect of environmentally induced variation of host-plant vigour on abundance of cereal aphids. In: Simon J.C., Dedryver C.A., Rispe C., Hulle M. (eds): Aphids in a New Millenium. Paris, Institute National de la Recherche Agronomique: 319–324.

Honek A., Martinkova Z., Lipavska H. (1998): Distribution of *Metopolophium dirhodum* in maize and cereals. In: Nieto-Nafria J.M., Dixon A.F.G. (eds): Aphids in Natural and Managed Ecosystems. Leon, Universidad de Leon: 569–578.

Honek A., Jarosik V., Dixon A.F.G. (2006): Comparing growth patterns among field populations of cereal aphids reveals factors limiting their maximum abundance. Bulletin of Entomological Research, 96: 269–277.

Kerzicnik L.M., Peairs F.B., Harwood J.D. (2010): Implications of Russian wheat aphid, *Diuraphis noxia*, falling rates for biological control in resistant and susceptible winter wheat. Arthropod-Plant Interactions, 4: 129–138.

Kieckhefer R.W., Gellner J.L., Riedell W.E. (1995): Evaluation of the aphid-day standard as a predictor of yield loss caused by cereal aphids. Agronomy Journal, 87: 785–788.

Klueken A.M., Hau B., Ulber B., Poehling H.M. (2009): Forecasting migration of cereal aphids (Hemiptera: Aphididae) in autumn and spring. Journal of Applied Entomology, 133: 328–344.

Larsson H. (2005): A crop loss model and economic thresholds for the grain aphid, *Sitobion avenae* (F.), in winter wheat in southern Sweden. Crop Protection, 24: 397–405.

doi: 10.17221/3/2016-PPS

Law C.N., Sutka J., Worland A.J. (1978): A genetic study of day-length response in wheat. Heredity, 41: 185–191.

Leonova E., Pestsova E., Salina E., Efremova T., Röder M., Börner A. (2003): Mapping of the *Vrn-B1* gene in *Triticum aestivum* using microsatellite markers. Plant Breeding, 122: 209–212.

Leslie T., van der Werf W., Bianchi F.J.J.A., Honek A. (2009): Population dynamics of cereal aphids: influence of a shared predator and weather. Agricultural and Forest Entomology, 11: 73–82.

MacGillivray M.E., Anderson G.B. (1964): The effect of photoperiod and temperature on the production of gamic and agamic forms in *Macrosiphum euphorbiae* (Thomas). Canadian Journal of Zoology, 42: 491–510.

Milec Z., Tomková L., Sumíková T., Pánková K. (2012): A new multiplex PCR test for the determination of *Vrn-B1* alleles in bread wheat (*Triticum aestivum* L.). Molecular Breeding, 30: 317–323.

Milec Z., Sumíková T., Tomková L., Pánková K. (2013): Distribution of different *Vrn-B1* alleles in hexaploid spring wheat germplasm. Euphytica, 192: 371–378.

Mohler V., Ortiz-Islas S., Lukman R., William M., Worland A.J., van Beem J., Wenzel G. (2004): Genetic and physical mapping of photoperiod insensitive gene *Ppd-B1* in common wheat. Euphytica, 138: 33–40.

Niehoff B., Stäblein J. (1998): Vergleichende Untersuchungen zum Schadoptential der Getreideblattlausarten *Metopolophium dirhodum* (Wlk.) und *Sitobion avenae* (F.) in Winterweizen. Journal of Applied Entomology, 122: 223–229.

Nishida H., Yoshida T., Kawakami K., Fujita M., Long B., Akashi Y., Laurie D.A., Kato K. (2012): Structural variation in the 5' upstream region of photoperiod-insensitive alleles *Ppd-A1a* and *Ppd-B1*a identified in hexaploid wheat (*Triticum aestivum* L.), and their effect on heading time. Molecular Breeding, 31: 27–37.

Pánková K., Milec Z., Simmonds J., Leverington -Waite M., Fish L., Snape J.W. (2008): Genetic mapping of a new flowering time gene on chromosome 3B of wheat. Euphytica, 164: 779–787.

Sarma R.N., Gill B.S., Sasaki T., Galiba G., Sutka J., Laurie D.A., Snape J.W. (1998): Comparative mapping of the wheat chromosome 5A Vrn-A1 region with rice and its relationship to QTL for flowering time. Theoretical and Applied Genetics, 97: 103–109.

Sengonca C., Hoffmann A., Kleinhenz B. (1994): Laboruntersuchungen zur Entwicklung Lebensdauer und Fruchtbarkeit der Getreideblattlausarten *Sitobion avenae* (F.) und *Rhopalosiphum padi* (L.) (Hom. Aphididae) bei verschiedenen tieferen Temperaturen. Journal of Applied Entomology, 117: 224-233.

Shindo C., Tsujimoto H., Sasakuma T. (2003): Segregation analysis of heading traits in hexaploid wheat utilizing recombinant inbred lines. Heredity, 90: 56–63.

Systat Software (2006): SigmaStat 3.5 User's Manual. Point Richmond, Systat Software Inc.

Simon J.C., Dedryver C.A., Pierre J.S., Tanguy S., Wegorek P. (1991): The influence of clone and morph on the parameters of intrinsic rate of increase in the cereal aphids *Sitobion avenae* and *Rhopalosiphum padi*. Entomologia Experimentalis et Applicata, 58: 211–220.

Tottman D.R., Broad H. (1987): The decimal code for the growth stages of cereals, with illustrations. Annals of Applied Biology, 110: 441–454.

UKZUZ (2015): Obilniny a luskoviny 2015. Available at http://eagri.cz/public/web/ukzuz/portal/odrudy/seznam-doporucenych-odrud/x2015/obiloviny-a-luskoviny.html

Vereijken P.H. (1979): Feeding and multiplication of three cereal aphid species and their effect on yield of winter wheat. Agriculture Research Reports, 888: 1–58.

Wetzel T. (2004): Integrierter Pflanzenschtz und Agroökosysteme. Pausa/Vogtland, Steinbeis-Transferzentrum (STZ).

Vickerman G.P., Wratten S.D. (1979): The biology and pest status of cereal aphids in Europe: a review. Bulletin of Entomological Research, 69: 1–32.

Welsh J.R., Keim D.L., Pirasteh B., Richards R.D. (1973): Genetic control of photoperiod response in wheat. In: Sears E.R., Sears L.M.S. (eds): Proceedings 4th International Wheat Genetics Symposium, Aug 6–11, 1973, Missouri Agricultural Experimental Station, Columbia, USA: 879–884.

White T.C.R. (2015): Senescence-feeders: a new trophic subguild of insect herbivores. Journal of Applied Entomology, 139: 11–22.

Yasue Y., Kawada K. (1969): The role of photoperiod and temperature in relation to population density on the wing development of the cabbage aphid, *Brevicoryne brassicae* L. Berichte des Ohara Instituts für Landwirtschaftliche Biologie, Okayama Universität, 15: A4.

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