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Host-plant mediated influences on population development of *Sitobion avenae* (Sternorrhyncha: Aphididae)

ALOIS HONĚK and ZDENKA MARTINKOVÁ

Research Institute of Crop Production, Drnovská 507, CZ-16106 Praha-Ruzyně, Czech Republic

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Abstract. We investigated the effects of genetic differences and host plant density on population development of the rose-grain aphid *Sitobion avenae* (F.) (Sternorrhyncha: Aphididae) in winter wheat stands. Aphid numbers on ears were recorded on 11 cultivars (6 years) and on plots where crop density was varied by thinning (12 years). Crop density significantly affected whole plant, tiller and ear mass, number of tillers, and leaf area and chlorophyll content. The duration and rate of aphid population growth, and the maximum numbers of aphids were ascertained by weekly counts. Maximum abundances increased with the length of time available for the growth of aphid populations while the rate of population growth was less important. Variation of maximum numbers of *S. avenae* on different cultivars was not significant, probably due to the small variation in the period available for the development of aphid populations. By contrast, there was a significant variation of aphid performance associated with host plant density. Aphid populations on solitary plants persisted longer and became more abundant than in dense stands. The prolonged survival of aphid populations was probably caused by an extended period of tillering and lower average age of tillers of solitary plants. There was large annual variation in aphid abundance. It is likely that modifications of host plant development caused by differences in winter weather may contribute to this variation.

INTRODUCTION

The aphid *Sitobion avenae* (F.) is important, due to its nearly worldwide distribution and damage caused to cereal crops (Vereijken, 1979; Wratten et al., 1979). It is an ear-inhabiting species in central and southern Europe while in the atlantic climate of western and northern Europe it is largely replaced by *Rhopalosiphum padi* (L.) (Carter & Rabbinge, 1980; Wiktelius & Ekbom, 1985; Leather, 1993). Typically, sexual reproduction and overwintering occurs on grass, but in regions with mediterranean or oceanic climate virginoparae may survive on winter cereals (Pons et al., 1995). As winter survival of virginoparae depends on temperature (Höller, 1990; Kleinholz & Şengonca, 1993) in the western Czech Republic anholocycly is exceptional, limited to stands of winter rye and years with very mild winters (Honěk, 1987). Migrants enter cereal stands in late May or early June and establish small colonies on leaves. After ear emergence, the aphids move to the ears where, together with late migrants, they establish abundant colonies. Typically, two generations are produced, whose birth and emigration rates determine maximum abundance (Rabbinge et al., 1979).

Maximum aphid abundance is determined by three demographic factors: magnitude of the immigrant population and duration and rate of population growth. Immigration rates are probably of less importance. An artificial increase in the initial numbers of *S. avenae* in wheat stands had a low effect on maximum aphid abundance (Entwistle & Dixon, 1989). By contrast, the length of the period available for population growth (time elapsed from establishing *S. avenae* populations on ears to attaining their peak densities), and the rate of population growth vary between years and stands (Entwistle & Dixon, 1986; Honěk, 1987). The variation is due to differences in aphid natality and rates of emigration affected by host plant quality (Watt, 1979; Pons & Tatchell, 1995), and mortality due to enemies and abiotic factors (Jones, 1979; Acreman & Dixon, 1986; Holz & Wetzel, 1990). Variation in host plant quality is an important determinant of *S. avenae* population development. The sources of variation in host plant quality are (i) genetic differences and (ii) environmental effects among which agronomic conditions have a prominent influence. Their relative importance is under dispute. The importance of genetic differences was shown by several authors (Lowe, 1984; Niraz et al., 1985; DiPietro & Dedryver, 1986; Leszczynski, 1987; Ciepiela, 1989; Havlíčková, 1989; Leszczynski & Dixon, 1990), and much attention was focused upon selecting aphid-resistant varieties. By contrast the variation caused by environmental effects has been little investigated.

In this paper we investigate the relative importance of genetic differences (cultivar) and crop density (a factor which modifies host plant stature and rate of maturation) for aphid population development. The comparison is based on a six-year study of aphid populations on winter wheat cultivars and a twelve-year study of host plants grown in dense or thinned stands.

MATERIAL AND METHODS

Genetic (cultivar) effects

Abundance of *S. avenae* was recorded from 1989 to 1994 at the Central Cereal Testing Station at Sedlec (50°10′N, 14°30′E), 5 km north of Praha. The experimental area is flat, situated on deep chernozem soil where local conditions are optimum for wheat growing. When growing plants, maximum care was paid to standardization of the cultivation. The experimental stands were grown in the 4th year of a 10-year crop rotation system, after alfalfa, and fertilized with 120, 120, and 160 kg ha^{-1} of N, P and K, respectively, sown between October 7–15 and grown using recommended agricultural practices. The observations were made in the stands grown under the regime of the State Cultivar Test Experiment which was a monofactorial experiment consisting of five incompletely randomized blocks, each of which contained 30 treatments (cultivars). The parallel 7 m wide blocks (separated one from the other by a 5 m space) were divided into 1.4 × 7 m (10 m^2) plots, each of which was sown with one of 30 tested cultivars (replicate). Only two blocks where aphid counts were made were left without insecticide treatment, in all experiment years. For each cultivar, numbers of *S. avenae* were therefore recorded in two replicates, at fixed places situated at 1.5 m distance from the short margin of the experimental plot, on 20 or 30 ears. The average aphid numbers were calculated for each date of observation and these figures used for calculating parameters of aphid population development. Recording aphid abundances began in 1989, with 30 established cultivars and origins. The collection of cultivars included in the State Cultivar Test Experiment changed each year so that after 6 years, the number of cultivars sown in all years of observation decreased to 11: Hana, Ilona, Livia, Regina, Senta, Simona, Sofia, Sparta, Viginta, Vlada, and Zdar.

Effects of crop density

The effect of developmental variation of host plant quality was investigated from 1987 to 1998 in production stands at Praha-Ruzyně (50°06′N, 14°16′E) where cultivars Mara (included in cultivar experiment for 4 years, average population parameters were not significantly different from the mean for 11 cultivars reported in this study, Honěk, unpubl.), Regina, Viginta and Zdar were grown in different years. Since the differences between cultivars were not significant the data from all years were pooled. Experimental plots of 5 × 5 m were established within crop stands, between March 14–25, at the late stage 2 – tillering (Zadoks' scale) (Tottman & Makepeace 1979). The crop density at plots either approached optimum recommended for wheat growing, 400–500 fertile tillers m^{-2} at the time of crop maturation (dense stands DEN), or the plants were thinned and the experimental plots then contained solitary plants standing 40–70 cm one from the other (solitary plants SOL). In 1987–1993 there were different numbers of SOL and DEN plots, in 1994–1998 the experiment design was standard including 3 DEN and 3 SOL plots. At the time of aphid presence, plant quality was recorded at 14 d intervals when 20 randomly selected tillers were cut on each plot and the height, mass and leaf area of tillers were established. In 1990–1993 whole plants with roots were extracted at the early ripening stage and their root to shoot (R/S) ratio and number of tillers per plant were de-

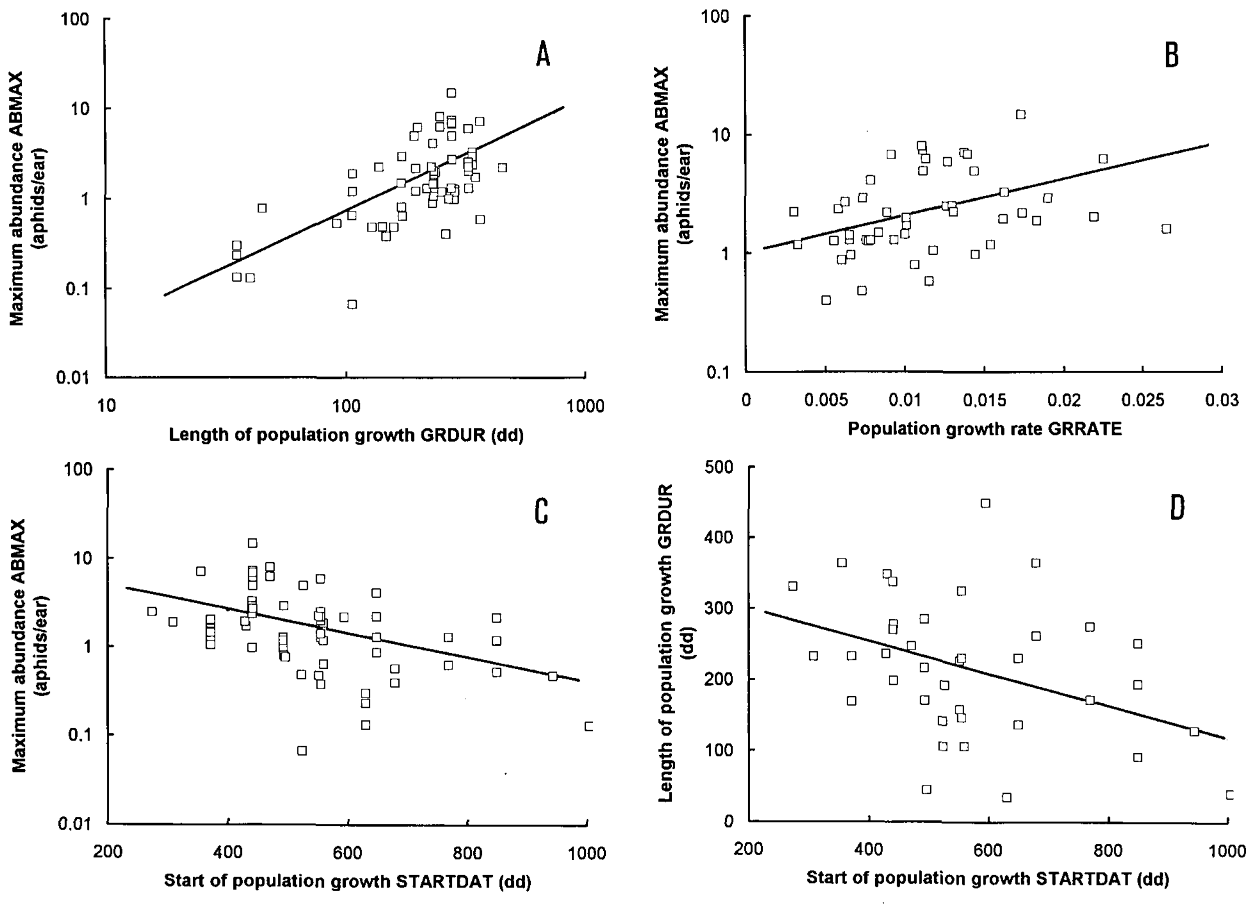

Fig. 1. Factors of maximum *S. avenae* abundance (ABMAX) on 11 cultivars. A – the length of the period of population growth GRDUR (log ABMAX = 1.153 logGRDUR – 2.481, F = 40.0, P < 0.001, df = 64); B – growth rate of *S. avenae* population GRRATE (log ABMAX = 29.99 GRRATE + 0.006, F = 8.52, P < 0.01, df = 46); C – timing of the onset of *S. avenae* population growth in the ears STARTDAT (log ABMAX = –0.0013 STARTDAT + 0.891, F = 16.12, P < 0.01, df = 64); D – the regression of GRDUR on STARTDAT (GRDUR = –0.217 STARTDAT + 343.4, F = 9.88, P < 0.01, df = 64). For explanation of acronyms see Material and methods.

TABLE 1. Annual variation (mean ± SE) of the parameters of *S. avenae* population development on 11 cultivars. The experiment of Sedlec. See Material and methods for explanation of acronyms.

	ABMAX	STARTDAT	ENDDAT	GRDUR	GRRATE
1989	6.89 ± 0.90	446.3 ± 12.1	711.8 ± 7.2	265.5 ± 13.8	0.0089 ± 0.0012
1990	1.70 ± 0.27	478.6 ± 13.4	759.5 ± 9.6	281.1 ± 18.2	0.0147 ± 0.0024
1991	1.62 ± 0.14	367.7 ± 16.3	586.8 ± 8.9	219.1 ± 20.6	0.0082 ± 0.0011
1992	2.21 ± 0.48	588.7 ± 14.3	846.7 ± 18.4	258.0 ± 21.8	0.0113 ± 0.0019
1993	1.03 ± 0.21	802.9 ± 36.4	1,023.7 ± 16.9	220.8 ± 35.7	0.0153 ± 0.0024
1994	0.97 ± 0.28	547.7 ± 19.5	661.6 ± 3.2	113.9 ± 19.4	0.0129 ± 0.0013
Mean	2.40 ± 0.31	538.7 ± 18.9	765.0 ± 18.1	226.4 ± 11.2	0.0114 ± 0.0007

termined. Since 1997 chlorophyll content of leaves was measured optically, by Chlorophyll Meter SPAD-502 (Minolta). Aphids were counted each time at four randomly selected sites within each plot, on 50–300 ears depending on aphid abundance.

Aphid counts

The counts were made at weekly intervals from ear emergence until no aphids remained. The calendar dates were transformed to numbers of day degrees (dd) above a 5°C threshold, summed from January 1, hereafter referred to as "biological time". Meteorological data were obtained from the observatories of the Central Cereal Testing Station at Sedlec and the Research Institute of Crop Production at Praha-Ruzyně, both cca 1 km from the experimental fields. Maximum abundance (maximum number of aphids per ear, ABMAX), time of settling of first aphids in ears (STARTDAT), time when maximum abundance was attained (ENDDAT), duration of growth of aphid population (GRDUR = ENDDAT – STARTDAT) and the rate of aphid population growth during the period of monotonical increase of aphid numbers (GRRATE, calculated as a slope of linear regression of log (n + 0.01) on biological time, where n is mean number of aphids per ear) were recorded.

Data processing

The analysis included two steps: (i) Establishing parameters of population development important for determination of maximum abundance ABMAX. This was done by calculating partial correlations between ABMAX and parameters of aphid population development, GRDUR and GRRATE. (ii) Investigating the magnitude of annual and host plant associated variation of ABMAX, GRDUR and GRRATE. This was done by ANOVA. To compensate for annual variation of aphid abundance the data were standardized, i.e. recalculated as percentage of the quantity attained in a given year on the plot where the aphid population was maximum. The percentage data were not transformed since their distribution was identical with raw data. The percentage of variance explained by an experimental factor was calculated as [SS factor /(SS error + SS factor)] × 100. The calculations were made using STATISTICA for Windows (StatSoft, 1994).

RESULTS

Effect of cultivar

The importance of plant genetic variation for development of *S. avenae* populations was investigated by testing the differences between cultivars. The stature of different cultivars grown in dense stands varied little. The minimum and maximum average length and weight of mature tillers in particular years varied by 4–7%, the average time of full ripeness differred by 3 days (average values of experiments at Central Breeding Station at Sedlec, Vladimír Beránek, pers. comm.).

Maximum aphid abundance ABMAX (Fig. 1) was related to the duration of population growth GRDUR (partial $R^2 = 0.4186$, $P < 0.01$) and population growth rate GRRATE (partial $R^2 = 0.1592$, $P < 0.05$). Multiple regression explained $R^2 = 0.4453$ ($P < 0.01$) variance. GRDUR significantly increased with earlier aphid settling on ears (decreasing STARTDAT, $R^2 = 0.1340$, $P < 0.05$) but was not affected by timing of population peak ENDDAT ($R^2 = 0.0571$, N.S.).

TABLE 2. Variation between cultivars (mean ± SE) of the parameters of *S. avenae* population development, average data from 1989–1994. The experiment of Sedlec. See Material and methods for explanation of acronyms.

	ABMAX	STARTDAT	ENDDAT	GRDUR	GRRATE
Livia	2.56 ± 0.98	540.2 ± 98.5	741.5 ± 68.6	201.3 ± 43.0	0.0148 ± 0.0029
Hana	3.90 ± 2.18	507.2 ± 44.4	771.1 ± 71.4	264.0 ± 50.5	0.0111 ± 0.0022
Ilona	2.49 ± 0.99	522.7 ± 70.0	764.5 ± 52.4	241.8 ± 33.0	0.0127 ± 0.0019
Vlada	1.87 ± 1.06	512.0 ± 55.2	758.6 ± 54.9	247.2 ± 34.5	0.0078 ± 0.0015
Sparta	2.58 ± 0.89	519.5 ± 70.0	740.0 ± 56.3	220.5 ± 24.2	0.0119 ± 0.0029
Sofia	2.95 ± 1.17	563.3 ± 84.9	786.4 ± 69.1	223.1 ± 48.6	0.0115 ± 0.0014
Viginta	2.35 ± 1.16	555.5 ± 60.9	780.6 ± 79.0	225.2 ± 45.9	0.0097 ± 0.0022
Senta	1.75 ± 0.37	556.3 ± 69.0	781.6 ± 65.2	225.4 ± 42.3	0.0133 ± 0.0041
Simona	1.85 ± 0.66	540.7 ± 55.2	770.3 ± 66.3	229.6 ± 33.6	0.0079 ± 0.0013
Regina	2.21 ± 0.84	527.9 ± 49.6	754.6 ± 62.9	226.7 ± 38.3	0.0148 ± 0.0025
Zdar	1.93 ± 0.65	580.2 ± 64.0	766.0 ± 62.3	185.8 ± 31.0	0.0110 ± 0.0017
Mean	2.40 ± 0.31	538.7 ± 18.9	765.0 ± 18.1	226.4 ± 11.2	0.0114 ± 0.0007

TABLE 3. One-way ANOVA of annual variation of parameters of *S. avenae* population development, established on 11 cultivars in 1989–1994. The experiment of Sedlec. See Material and methods for explanation of acronyms.

	SS effect	df	MS effect	SS error	df	MS error	F	P
ABMAX	277.18	5	55.44	137.82	60	2.30	24.13	< 0.001
STARTDAT	1,250,094.0	5	250,198.9	274,962.0	60	4,582.7	54.59	< 0.001
ENDDAT	1,307,835.0	5	261,566.9	94,070.5	60	1,567.8	166.8	< 0.001
GRDUR	200,811.6	5	40,162.2	338,188.0	60	5,636.5	7.125	< 0.001
GRRATE	0.000320	5	0.000064	0.000907	42	0.000022	2.964	< 0.05

TABLE 4. One-way ANOVA of variation of parameters of *S. avenae* population development due to cultivar differences, established on 11 cultivars in 1989–1994. The experiment of Sedlec. See Material and methods for explanation of acronyms.

	SS effect	df	MS effect	SS error	df	MS error	F	P
ABMAX	23.29	10	2.33	391.70	55	7.13	0.327	> 0.05
APHDAY	500,122.7	10	50,012.3	9,500,347.0	55	172,733.6	0.290	> 0.05
STARTDAT	32,249.5	10	3,225.0	1,493,707.0	55	27,158.3	0.119	> 0.05
ENDDAT	14,244	10	1,424.4	1,387.661.0	55	25,230.2	0.056	> 0.05
GRDUR	26,513.4	10	2,651.3	512,485.6	55	9,317.9	0.285	> 0.05
GRRATE	0.000247	10	0.000025	0.000980	37	0.000026	0.933	> 0.05

TABLE 5. One-way ANOVA of standardized variation of maximum aphid abundance (ABMAX) as affected by 11 cultivars (the experiment of Sedlec, 1989–1994) and by variation of host plant quality (the experiment of Praha-Ruzyně, 1987–1998).

	SS effect	df	MS effect	SS error	df	MS error	F	P
Cultivar	0.6600	10	0.0660	4.263	55	0.7752	0.8514	> 0.05
Plant quality	2.7473	1	2.7473	4.1052	59	0.0696	39.484	< 0.001

ABMAX and parameters of aphid population development varied greatly with years (Table 1) but differed little between the cultivars (Table 2). The one-way ANOVA (Table 3) revealed that annual variation explained 67%, 82%, 93%, 37% and 26% of ABMAX, STARTDAT, ENDDAT, GRDUR and GRRATE variance, respectively (for calculations see Material and methods). Genetic variation associated with cultivar differences was not significant and explained only 1–20% of the variance of aphid population parameters (Table 4). After standardization, the differences between cultivars were also not significant and accounted for only 13.4% of ABMAX variance (Table 5).

Effect of host plant quality

The differences in crop density caused variation in host plant quality and differences in *S. avenae* performance. SOL plants had a significantly greater number of tillers per plant, tiller mass, ear mass, leaf area and chlorophyll content than DEN plants (Table 6). The variation was caused by intraspecific competition in DEN stands that caused shortening of the tillering period, greater investments into stem elongation and earlier mortality of lower leaf strata. Extended tillering period in SOL plants resulted into decreasing average tiller age at the time of aphid presence.

Maximum *S. avenae* abundances ABMAX were positively correlated (Fig. 2) with the duration of population growth GRDUR (partial $R^2 = 0.1132$, $P < 0.01$) and population growth rate GRRATE (partial $R^2 = 0.1062$, $P < 0.01$), and both factors explained $R^2 = 0.1748$ variance ($P < 0.01$). ABMAX varied with years (Fig. 3) and also differed significantly between dense crop stands and solitary plants (Table 5). The one-way ANOVA of effects of host plant quality calculated for non-standardized data of 1994–1998 revealed significant variation of ABMAX (24.9% variance explained) and GRDUR (19.1%) (Table 7). Annual variation in 1994–1998 was highly significant and explained 53.4% of ABMAX variance ($F_{4,25} = 7.149$, $P < 0.001$). The ANOVA performed on standardized 1994–1998 data confirmed a significant effect of plant quality on ABMAX (52.8% variance explained, $F_{1,28} = 31.309$, $P < 0.001$) and GRDUR (29.2%, $F_{1,28} = 11.522$, $P < 0.01$), but the effect on STARTDAT (15.8%, $F_{1,28} = 5.254$, $P < 0.05$) was also significant. Aphid abundances in 1994–1998 were low and this may account for the low significance of GRRATE in this period.

DISCUSSION

Relative importance of parameters of aphid population development

The maximum abundance of *S. avenae* in winter wheat ears was determined by both duration and rate of population growth. The importance of these factors differed when aphid performance was varied by cultivar and differences in host plant quality caused by crop density. In the former case, time available for population growth (GRDUR) was correlated with the rate of aphid population growth (GRRATE). By contrast, in the latter case GRDUR and GRRATE varied independently and a joint occurrence of a long period of population growth and a

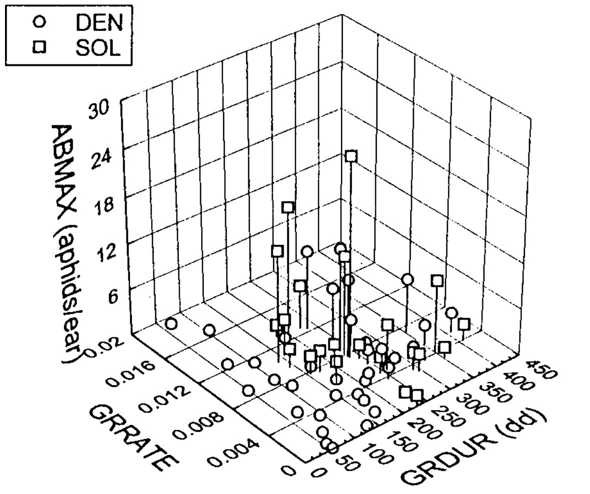

Fig. 2. Factors of maximum *S. avenae* abundance (ABMAX) when host plant quality was varied by environment effects during earlier plant development (logABMAX = 0.018 GRDUR + 400.31 GRRATE – 2.8783, R = 0.4180, $F_{2,58}$ = 6.1415, P < 0.05). For explanation of acronyms see Material and methods.

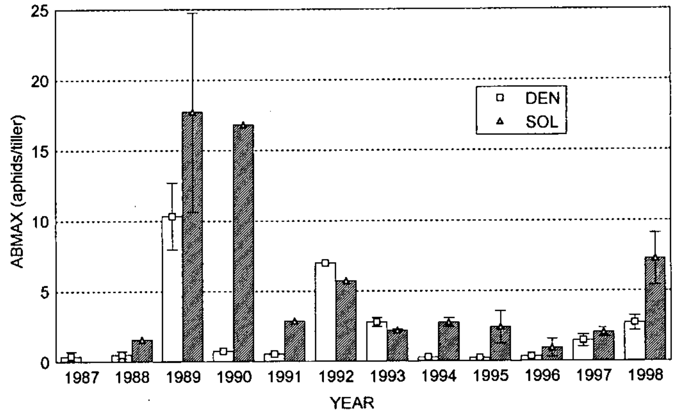

Fig. 3. Annual variation of ABMAX in DEN (open bars) and SOL (solid bars) plants. For explanation of acronyms see Material and methods.

high growth rate was a precondition for development of abundant aphid populations. The factors affecting the abundance of *S. avenae* are similar to those influencing the populations of *Metopolophium dirhodum* (Walker) (Honěk, 1991a) but the importance of variation in population growth rate is greater in *S. avenae*. The importance of the GRDUR indicated that time available for aphid population growth is a factor which limits maximum abundance. Retarding plant maturation and increasing the time spent in stages 6 (anthesis) – 8 (dough development) (Zadoks' scale) increases the likelihood of *S. avenae* developing large populations.

Relative importance of cultivar and host plant quality in determining *S. avenae* abundance

Genetic variation (differences between cultivars) did not seriously affect *S. avenae* population development (cf. Dedryver & DiPietro, 1986). This may be due to the choice of cultivars included in this study. Modern cultivars have a similar level of resistance, lower compared to old cultivars (Sotherton & Lee, 1988; cf. Şengonca et al., 1994). By contrast, crop density that varied plant quality was an important factor of *S. avenae* abundance (Honěk, 1987; 1991b, c). Intraspecific competition is proportional to wheat stand density (number of tillers per area) which is determined not only by the number of germinating seeds but also the number of tillers produced per plant.

TABLE 6. Selected characteristics (mean ± SE) of winter wheat plants grown in dense stands (DEN) and solitary (SOL), about 1 week before aphid population peak. Data of 1990 and 1993 (R/S ratio and number of tillers) and 1997 (other characters), experiment of Praha-Ruzyně.

	DEN	SOL
Root/shoot ratio × 100	7.36 ± 0.57	7.84 ± 0.67
Number of tillers plant^{-1}	1.9 ± 0.3*a*	8.3 ± 1.1*a*
Tiller height (cm)	60.0 ± 2.4	55.0 ± 2.4
Tiller mass (g)	2.14 ± 0.07*a*	2.55 ± 0.08*a*
Ear mass (g)	0.81 ± 0.02*a*	0.99 ± 0.08*a*
Leaf area tiller^{-1}	33.8 ± 2.5*a*	41.8 ± 2.9*a*
Chlorophyll content (SPAD units)	51.8 ± 0.5*a*	55.2 ± 0.4*a*

a – data accompanied by the same letter are different at P < 0.05.

Plants of dense stands consist typically of 2–3 fertile tillers, those which have appeared and will mature first. Solitary growth allows abundant tillering. Prolonged tillering decreases average tiller age and extends the time available for aphid presence in ears. The aphids may not only stay longer before the onset of ear senescence (increasing GRDUR) but also make better use of the higher food quality of the "juvenilised" host plant (increasing GRRATE).

Why variation of plant quality caused by crop density is so important in winter wheat?

We propose that not only the magnitude of differences caused by variations in crop density but also the timing of their origin was important for determining *S. avenae*

TABLE 7. One-way ANOVA of variation in maximum abundance and parameters of aphid development as varied by host plant density. Data of 1994–1998, not standardized, experiment of Praha-Ruzyně. See Material and methods for explanation of acronyms.

	SS effect	df	MS effect	SS error	df	MS error	F	P
ABMAX	32.261	1	32.261	97.211	28	3.472	9.2922	< 0.01
STARTDAT	22413.3	1	22413.3	470539.3	28	16805.0	1.3337	> 0.05
ENDDAT	4762.8	1	4762.8	591563.9	28	21127.3	0.2254	> 0.05
GRDUR	47840.1	1	47840.1	202197.9	28	7221.4	6.6249	< 0.05
GRRATE	0.000015	1	0.000015	0.000263	28	0.000009	1.6361	> 0.05

population dynamics. The stature of solitary and dense stand plants was established before aphid immigration and the differences only continued and increased during the period of aphid presence on host plants. The large effect of early development conditions on plant stature (mass, leaf area) and the persistence of the modifications until plant death is typical for (winter) annuals including wheat and other small grain cereals. This characteristic feature of annuals increases the importance of developmental modifications of plant stature for determining aphid abundance. Environmental effects on host plant stature thus may become more important than variation between cultivars. Unlike annuals, perennials and trees may compensate for environmental effects accumulated in one season during the following years and the development factors may have a less important role.

In winter wheat, the effects of early developmental changes mediated by the host plant may have a dual influence on variation in aphid performance. First, they increase local variation in aphid population dynamics as it is evident in stands of different quality. However, it seems that plant developmental changes may also contribute to the annual variation of aphid numbers. Duration of the period suitable for aphid population growth may be influenced by the heterochrony of biological time of winter wheat and *S. avenae*, caused by different temperature requirements. The temperature threshold for development of the investigated winter wheat cultivars is approx. +0.8°C (L. Bláha, pers. comm.), the lower development threshold for aphids is approx. +5°C (Dean, 1974; Honěk & Kocourek, 1990; Honěk, 1996). So there is about a 4°C temperature "window" where, during the winter and early spring, winter wheat plants may grow and develop while development of *S. avenae* populations is inhibited by low temperature. The combined effects of temperature and water availability during this period may cause variation in winter wheat development that affects synchrony in the timing of winter wheat development and aphid presence. This heterochrony may in consequence decrease the time available for *S. avenae* presence in ears and contribute to annual variation in aphid abundance.

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REFERENCES

ACREMAN T.M. & DIXON A.F.G. 1986 The role of awns in the resistance of cereals to the grain aphid Sitobion avenae. *Ann. Appl. Biol.* **109**: 375–381.

CARTER N. & RABBINGE R. 1980: Simulation models of the population development of Sitobion avenae. *IOBC WPRS Bull.* **3**: 93–98.

CIEPIELA A. 1989: Biochemical basis of winter wheat resistance to the grain aphid, Sitobion avenae. *Entomol. Exp. Appl.* **51**: 269–275.

DEAN G.J. 1974: Effect of temperature on the cereal aphids Metopolophium dirhodum (Wlk.), Rhopalosiphum padi (L.) and Macrosiphum avenae (F.) (Hem., Aphididae). *Bull. Entomol. Res.* **63**: 401–409.

DEDRYVER C.A. & DIPIETRO J.P. 1986: Biologie des pucerons des céréales dans l'Ouest de la France. VI. Etude comparative des fluctuations au champ des populations de Sitobion avenae (F.), Metopolophium dirhodum (Wlk.) et Rhopalosiphum padi (L.) sur différentes cultivars de blé d'hiver. *Agronomie* **6**: 75–84.

DIPIETRO J.P. & DEDRYVER C.A. 1986: Relations entre les pucerons des céréales et leurs plantes-hôtes. I. Mise au point d'une méthodologie de recherche de résistance à Sitobion avenae (F.) chez différentes cultivars de blé d'hiver. *Agronomie* **6**: 469–479.

ENTWISTLE J.C. & DIXON A.F.G. 1986: Short-term forecasting of peak population density of the grain aphid (Sitobion avenae) on wheat. *Ann. Appl. Biol.* **109**: 215–222.

ENTWISTLE J.C. & DIXON A.F.G. 1989: The effect of augmenting grain aphid (Sitobion avenae) numbers in a field of winter wheat in spring on the aphids abundance in summer and its relevance to the forecasting of outbreaks. *Ann. Appl. Biol.* **114**: 397–408.

HAVLÍČKOVÁ H. 1989: (Differences in the degree of invasion of winter wheat varieties by cereal aphids under field conditions.) *Ochrana Rostlin* **25**: 53–58 (in Czech).

HÖLLER C. 1990: Overwintering and hymenopterous parasitism in autumn of the cereal aphid Sitobion avenae (F.) in northern FR Germany. *J. Appl. Entomol.* **109**: 21–28.

HOLZ F. & WETZEL T. 1989: Einschatzung und Nutzung eines Populationsmodells fur die Getreidelaus Macrosiphum (Sitobion) avenae (F.). *J. Appl. Entomol.* **108**: 328–334.

HONĚK 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). *J. Appl. Entomol.* **104**: 304–314.

HONĚK A. 1991a: Factors determining the peak abundance of Metopolophium dirhodum (Homoptera, Aphididae) on cereals. *Bull. Entomol. Res.* **81**: 57–64.

HONĚK A. 1991b: Environment stress, plant quality and abundance of cereal aphids (Hom., Aphididae) on winter wheat. *J. Appl. Entomol.* **112**: 65–70.

HONĚK A. 1991c: Dry mass allocation in cereal plants and distribution of Metopolophium dirhodum and Sitobion avenae (Homoptera: Aphididae). *Acta Entomol. Bohemoslov.* **88**: 103–109.

HONĚK A. 1996: The relationship between thermal constants for insect development: a verification. *Acta Soc. Zool. Bohem.* **60**: 115–152.

HONĚK A. & KOCOUREK F. 1990: Temperature and development time in insects: a general relationship between thermal constants. *Zool. Jb. Syst.* **117**: 401–439.

JONES M.G. 1979: Abundance of aphids on cereals from before 1973 to 1977. *J. Appl. Ecol.* **16**: 1–22.

KLEINHOLZ B. & ŞENGONCA C. 1993: Das unterschiedliche Auftreten und die Vermehrung der Getreideblättlause auf Wintergerste und Winterweizen zweier aufeinanderfolgenden Herbst- und Winterperioden. *Mitt. Dtsch. Ges. Allg. Angew. Entomol.* **8**: 609–613.

LEATHER S. 1993: Overwintering in six arable aphid pests: a review with particular relevance to pest management. *J. Appl. Entomol.* **116**: 217–233.

LESZCZYNSKI B. 1987: Winter wheat resistance to the grain aphid Sitobion avenae (Fabr.) (Homoptera, Aphididae). *Insect Sci. Appl.* **18**: 251–254.

LESZCZYNSKI B. & DIXON A.F.G. 1990: Resistance of cereals to aphids: Interaction between hydroxamic acids and the aphid

Sitobion avenae (Homoptera: Aphididae). *Ann. Appl. Biol.* **117**: 21–30.

LOWE H.J.B. 1984: Characteristics of resistance to the grain aphid Sitobion avenae in winter wheat. *Ann. Appl. Biol.* **105**: 529–538.

NIRAZ S., LESZCZYNSKI B., CIEPIELA A., URBANSKA A. & WARCHOL J. 1985: Biochemical aspects of winter wheat resistance to aphids. *Insect Sci. Appl.* **3**: 253–257.

PONS X., COMAS J. & ALBAJES R. 1995: Occurrence of holocyclic and anholocyclic populations of Rhopalosiphum padi and Sitobion avenae (Hom., Aphididae) in the northeast Spain. *J. Appl. Entomol.* **119**: 171–175.

PONS X. & TATCHELL G.M. 1995: Drought stress and cereal aphid performance. *Ann. Appl. Biol.* **126**: 19–31.

RABBINGE R., ANKERSMIT G.W. & PAK G.A. 1979: Epidemiology and simulation of population development of Sitobion avenae in winter wheat. *Neth. J. Plant Pathol.* **85**: 197–220.

ŞENGONCA C., JOSCH H. & KLEINHENZ B. 1994: Einfluss verschiedener Wintergerste- und Winterweizensorten auf die Besiedelung und Populationsentwicklung von Getreideblättlausen. *Ges. Pfl.* **46**: 3–7.

SOTHERTON N.W. & LEE G. 1988: Field assessments of resistance to the aphids Sitobion avenae and Metopolophium dirhodum in old and modern spring-sown wheats. *Ann. Appl. Biol.* **112**: 239–248.

STATSOFT 1994: *Statistica. Vol. 1: General Conventions and Statistics*. StatSoft, Tulsa, pp. 1001–1718.

TOTTMAN D.R. & MAKEPEACE R.J. 1979: An explanation of the decimal code for the growth stages of cereals, with illustrations. *Ann. Appl. Biol.* **93**: 221–234.

VEREIJKEN P.H. 1979: Feeding and multiplication of three cereal aphid species and their effect on yield of winter wheat. PUDOC, Wageningen, 58 pp.

WATT A.D. 1979: The effect of cereal growth stages on the reproductive activity of Sitobion avenae and Metopolophium dirhodum. *Ann. Appl. Biol.* **91**: 147–157.

WIKTELIUS S. & EKBOM B.S. 1985: Aphids in spring sown cereals in central Sweden. Abundance and distribution 1980–1983. *J. Appl. Entomol.* **100**: 8–16.

WRATTEN S.D., LEE G. & STEVENS D.J. 1979: Duration of cereal aphid populations and the effects on wheat yield and quality. *Proceedings 1979 British Crop Protection Conference – Pests and Diseases 1*. British Crop Protection Council, Croydon, pp. 1–8.

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