

# Comparing growth patterns among field populations of cereal aphids reveals factors limiting their maximum abundance

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## Abstract

Cereal stands in central Europe are commonly infested with three species of aphids that may become serious pests. With increasing abundance, the proportion of a particular species in the total aphid population may remain constant, suggesting a density-independent exponential growth, or the proportion can change, suggesting density-dependent constraints on growth. The constraints that affect particular species, and thus their relative abundance, were studied. The proportionality between maximum abundances of the cereal aphids was studied using a 10-year census of the numbers of aphids infesting 268 winter wheat plots. For two species their abundance on leaves and ears was compared. With increasing aphid density the maximum abundance of *Rhopalosiphum padi* (Linnaeus) remained proportional, but not that of *Sitobion avenae* (Fabricius), which was constrained by the smaller surface area of ears compared to leaves. There was no evidence of inter-specific competition. Maximum abundance of *R. padi* and *Metopolophium dirhodum* (Walker) on leaves did not change proportionally as the proportion of *M. dirhodum* decreased with increasing overall aphid density. This decrease was probably caused by the restricted distribution of *M. dirhodum*, which is confined to leaves, where space is limiting. No change in proportion between populations was detected when the average densities were below 0.54 aphids per leaf or ear. Non-proportional relationships between aphid populations appeared to be due to spatial constraints, acting upon the more abundant population. Detecting the limitation of population growth can help with the assessment of when density-independent exponential growth is limited by density-dependent factors. This information may help in the development of models of cereal aphid population dynamics.

**Keywords:** population dynamics, maximum abundance, cereals, *Rhopalosiphum padi*, *Sitobion avenae*, *Metopolophium dirhodum*

## Introduction

In central Europe three species of aphid (Hemiptera: Aphididae) commonly infest winter wheat: *Metopolophium dirhodum* (Walker), which is the dominant species on leaves and avoids the ears, *Sitobion avenae* (Fabricius), dominant on ears but also lives on leaves and *Rhopalosiphum padi* (Linnaeus), which can colonize the whole plant. These aphids migrate to wheat, around mid-May, from their winter hosts: *Rosa* spp. (*M. dirhodum*), different Poaceae (*S. avenae*) and *Prunus padus* L. (*R. padi*). They initially colonize the leaves, and, after flowering, also the ears. Their populations grow and reach their maximum densities, usually in the last decade of June, and then sharply decline in abundance. The details of population development of cereal aphid species and the effect of host plant are well studied (e.g. Wratten, 1975; Leather & Dixon, 1981; Honek & Martinkova, 1999). Aphid populations on winter cereals are present for a short and well-defined period, grow monotonically and the maximum abundance is easy to detect. These short-lived aphid populations living on annual plants or winter annuals are a particularly convenient system for studying the general pattern of change in population numbers of coexisting species, or of the numbers of a species occurring on different parts of the same plant. Here a 10-year census of aphids on winter wheat tillers and a 6-year census of aphids on wheat ears are analysed.

For each species of aphid the maximum abundance attained varies both between years and plant organs. This variation is interesting because it may reveal factors that limit population growth of particular aphid species. If the proportion of the total aphid population made up of a particular species changes among years with different overall aphid abundance then this may be a consequence of specific limits placed on population growth of each species. However, it is difficult to detect the asymmetrical growth and change in proportions of two populations as overall density increases. The change may result from a constraint on the growth of one of the populations (e.g. spatial limitation or intra-population competition) or an interaction between the populations (e.g. inter-specific competition). There are few studies that show the results of these constraints under natural conditions (cf. Denno *et al.*, 1995). In the case of inter-population competition the populations often co-exist and their abundances are only slightly modified. Differences due to a constraint operating on one of the populations are rarely studied. Regression of the abundance of one species against that of another may demonstrate such an interaction (Hunter, 1998).

Here a new regression method for detecting constraints on population growth of cereal aphids is evaluated. The maximum abundances attained by two species living in the same place, or of one species living on different parts of the same plant, are compared. A non-proportional relationship is used to detect whether there are constraints acting on co-occurring populations. The growth of *R. padi* and *S. avenae* on leaves vs. ears, of *M. dirhodum* vs. *R. padi* and *M. dirhodum* vs. *S. avenae* on leaves, and *R. padi* vs. *S. avenae* on ears, was investigated. This was done in three steps: (i) those populations experiencing constraints were detected; (ii) the nature of the non-proportional relationship between populations was determined by means of regression of the maximum abundance of the less abundant population on

the more abundant population, and (iii) the course of growth of each of the populations was analysed to demonstrate the existence of constraints.

## Materials and methods

### *Detecting constraints on population growth*

The method of detecting constraints on population growth, applied to co-occurring aphid populations, is based on comparing aphid numbers in census data at maximum abundance. Populations of the same species, on ears and leaves, or populations of different species, either on leaves or ears, were compared, using the maximum abundance on ears and that on leaves for each species in each plot in each season. The proportions of the two populations may either remain constant, or change relative to one another, as total abundance increases. In the former case the relationship between populations is proportional and in the latter non-proportional. The proportionality was detected by determining the slope of the regression of the maximum numbers of one population on that of the other.

It is important to obtain an accurate estimate of the true regression slope. Model I regression ('standard' regression) should not be used because it assumes no error in the measurement of the explanatory ( $x$ ) variable and therefore underestimates the true slope. Major axis (Sokal & Rohlf, 1995) is the preferred procedure because it assumes an equal error in the  $x$  and  $y$  variables. For its accurate use, both axes must be similarly scaled (e.g. log-log scale).

Before the analysis the problem of detecting abundance at very low overall population densities was addressed. Under these circumstances there is no relationship between the populations at their maximum densities and natural constraints cannot be detected by regression analysis. This is the case when, in cereal aphids, the population density is too low to detect any increase (Jarosik *et al.*, 2003). Therefore, the data were first corrected for the underestimate in the values of the regression slopes due to including data for very low densities.

After correcting for this underestimate, changes in the relative abundance of two aphid populations can be demonstrated by plotting log maximum abundance of one population against the other, and by calculating the slope of this relationship. If the slope is equal to 1 the increase in the density of both populations is proportional, i.e. the species occur in similar proportions, regardless of whether they are scarce or abundant. If the slope of the regression line is smaller or greater than 1 the change is not proportional and one species becomes relatively scarce as the overall abundance increases.

Proportional or non-proportional relationships may result from several causes. One cause could be differences in population dynamics. Proportional relationships may (or may not) occur when both populations grow exponentially until they reach their maximum abundance. That is, their growth is density-independent. By contrast, disproportionate change may arise if the growth rate of both or one of the populations decreases before the maximum abundance is reached. That is, their growth is density-dependent. The population growth rates can be tested for density dependence and used to test the above concept.

### Aphid counts

Aphid densities were recorded at two localities in the Czech Republic. At Praha-Ruzyně (50°06'N, 14°17'E), aphids were counted on cultivars of winter wheat Hana, Regina, Viginta and Zdar, from 1987 to 1996. Each year, 5–15 experimental plots of c. 25 m<sup>2</sup> were established within each stand. A total of 107 plots were monitored. At Sedlec (50°10'N, 14°30'E), aphids were monitored in small (1.38 m × 7.27 m = 10 m<sup>2</sup>) experimental plots established for the routine testing of new cultivars, from 1989 to 1994. Aphid counts were made on 161 plots of 54 established and new cultivars.

Aphid counts were made weekly, or at 3–4 day (1990) intervals, from before aphid immigration until their disappearance from the crop. On each occasion, 30–300 tillers were examined depending on aphid abundance. Initially 300 tillers, chosen at random, were sampled but then sample size was adjusted to maintain a standard error of approximately 25% of the mean number of aphids per tiller (Southwood & Henderson, 2000). At Praha-Ruzyně, the aphids on leaves (including leaf sheaths) and on ears were recorded separately, except in 1991, when only those on the ears were recorded. The tillers were selected at random at 2–5 places within each experimental plot. At Sedlec, aphid numbers were recorded at two fixed places within each experimental plot, on 40 or 60 ears. At both localities, agricultural practices recommended for wheat growing in the Czech Republic were followed (Spaldon, 1982), except for the application of insecticide.

### Statistical procedures

#### Fitting regression to maximum abundances of species

To correct the underestimate in the values of the regression slopes at the very low densities, locally weighted regression scatterplot smoothing (LOWESS) regression (Cleveland, 1979; Chambers *et al.*, 1983) was used to determine the densities at which population growth started to be detectable. This was done by showing that there is a region of effective neutrality (Trexler & Travis, 1993), i.e. population densities below which there are no relationships between maximum aphid counts. This region was assessed by iterations of the LOWESS model. The iterations differed in local sensitivity expressed as a span of smoothing between 0–1. The region with no relationship between two populations was determined from two iterations that produced fits with the same general impression (Cleveland, 1979) and that had residuals with no pattern (Cleveland, 1985). The bias/variance trade off resulting from the smoothing procedure was checked using the methods of Hastie & Tibshirani (1990, Chapter 3). Other non-parametric techniques of smoothing, such as spline, polynomial and Gaussian kernel, were also applied, and produced very similar results to the LOWESS model. The smoothing process was done using S-PLUS (2001).

The existence of a region of effective neutrality was then verified by regressions between maximum aphid counts in this region. This was done using standard model I regression (the parametric least-square regression) and the randomization statistic. The randomization statistic was the correlation coefficient between counts from 10,000 randomizations. This statistic is equivalent to a regression coefficient with normally distributed errors in the ordinate

Table 1. Probability of rejecting a significant regression between maximum aphid counts in the section with no relationship between maximum counts (see figs 1 and 2), called 'section of neutrality'.

Species	N	F-test	ARC
<i>Sitobion avenae</i> , ears on leaves	5	96.0	100
<i>Rhopalosiphum padi</i> , ears on leaves	15	51.3	50.0
Total aphids	48	12.9	9.1
<i>R. padi</i> on <i>Metopolophium dirhodum</i> , leaves	5	68.2	50.0
<i>S. avenae</i> on <i>M. dirhodum</i> , leaves	40	10.7	9.2
<i>R. padi</i> on <i>S. avenae</i> , ears <sup>1</sup>	38	45.3	48.6
<i>R. padi</i> on <i>S. avenae</i> , ears <sup>2</sup>	9	41.7	42.9

<sup>1</sup> Praha-Ruzyně, <sup>2</sup> Sedlec.

Regressions were calculated by conventional least-square regression method (F-test, %) and from 10,000 randomizations (points for absolute regression coefficients ARC, %). N = number of observations.

(Manly, 1991). The use of LOWESS regression without verification by randomization tests is only partially justified because the LOWESS is a parametric test and assumes (as does the model I regression) no error in the *x* variable, which is incorrect in this analysis as there are errors in both axes. The use of the LOWESS regression was justified, because the conventional parametric least-square regression tests and randomization tests gave similar results (table 1). Consequently, the data looked as if it came from a normal distribution, and in that case a parametric test can be thought of as an approximation for a randomization test (Manly, 1991, p. 17).

The regression slopes were calculated only for data in which the relationship between the abundance of both populations was significant. To detect single-species limitations on different plant organs, maximum log aphid abundance of a species on the ears was regressed on maximum log aphid abundance of the same species on the leaves. Two-species relationships were calculated by regressions of maximum log abundance of one species on those of the other, separately on ears and leaves. The change in population abundance was evaluated as proportional if the 95% confidence interval of the major axis overlapped the slope 1. If the 95% confidence interval was greater or smaller than 1 the change was evaluated as non-proportional. Because we used only one count from each plot each year, and verified that the counts between plots and between years were not significantly correlated (Mantel tests; Sokal & Rohlf, 1995, p. 813–819), the errors in the regression analyses can be assumed to be random, independent variables.

#### Detecting variation in population dynamics

The differences in the population dynamics of single species underlying the variation in species proportions were tested for by fitting density-independent exponential growth, and density-dependent deviations from the exponential growth. This was assessed for each species each year on each plot, separately on ears and leaves. This was done by fitting a regression to population growth linearized by logarithmic transformation of the population size *N* on leaves or ears, and by expressing time in day-degrees (DD)

above the lower development threshold of 5°C (Honek & Kocourek, 1990; Honek, 1996) from the beginning of immigration to the time of the maximum aphid abundance. Then, the model corresponding to density-independent exponential growth was:

$$\ln[N_{DD}] = \ln[N_0] + b * DD \quad (1)$$

where  $N_{DD}$  is the response variable, number of aphids at time  $DD$ ,  $N_0$  is the intercept,  $b$  is the slope of the regression line and the population growth rate, and  $DD$  is an explanatory variable, the sampling date – time in day degrees. To test for deviations from density-independent exponential growth, we tested for deviation from linearity using second order polynomial regression. The square of the explanatory variable was calculated and subtracted from regression (1):

$$\ln[N_{DD}] = \ln[N_0] + b_1 * DD - b_2 * DD^2 \quad (2)$$

If the subtraction caused a significant reduction in deviance, there was evidence of density-dependent deviation from exponential growth.

Calculations of equations 1 and 2 were made using general linear modelling in GLIM (Francis *et al.*, 1994). The use of log aphid counts and normal distribution of errors appeared preferable to using generalized linear models with Poisson or negative binomial distribution of errors (McCullagh & Nelder, 1989). It was confirmed by testing these distributions using aphid counts made in 1997 and 1999, years that had low and high aphid abundance, respectively. The observed distributions differed significantly both from Poisson and negative binomial distributions. In addition, the residual deviances were generally larger and the explanatory powers generally smaller for the models using Poisson or negative binomial errors than for those using log transformation and normal errors. The adequacy of the models with log aphid counts and normal distribution of errors was further checked by plotting standardized residuals against fitted values and against explanatory variables, and the ordered residuals against expected order statistics (Crawley, 1993).

## Results

### Onset of population growth

The plots of maximum aphid densities revealed that proportional differences between populations could not be established (table 1) when maximum abundance was very low (figs 1 and 2). The maximum abundance of populations grew in parallel only after they exceeded a certain threshold density. The data sets each have two sections, the uncorrelated data when aphid abundance was low, and correlated data when the maximum abundance exceeded the threshold density. The uncorrelated segment of data mostly included cases where recently established aphid populations did not persist and increase. Consequently, no change in proportion between populations was detected at very low densities.

For single species situations, the average threshold densities for *Sitobion avenae* were 0.13 per leaf and 0.61 per ear, and for *Rhopalosiphum padi* 0.37 per leaf and 0.22 per ear. For populations of two species on the same plant organ, the threshold densities were 0.68 per leaf when *M. dirhodum* was evaluated together with *R. padi* and 1.65 per leaf when with *S. avenae*; for *R. padi*, 0.22 per leaf and 0.25

per ear, and *S. avenae*, 0.37 per leaf and 0.90 per ear, respectively.

### Single species on different plant organs

When the maximum abundances exceeded the threshold density, the numbers of *S. avenae* on ears and leaves were non-proportional, while those of *R. padi* remained proportional as maximum abundances increased (fig. 1). As a consequence, for *S. avenae* the relationship between the regression slopes of maximum numbers on ears vs. that on the leaves was significantly smaller than 1 (table 2), with a slope=0.42 and 95% confidence interval 0.28–0.60. The cause was the difference in the rate of population growth, which was exponential on leaves, indicating the absence there of a limit on population increase. However, on the ears, there were negative deviations from exponential growth as density increased; the population growth appeared curvilinear and the growth decreased as the density increased (fig. 3). This was assisted by *S. avenae* moving on to the ears, where they became more abundant than on the leaves (one-way ANOVA:  $F=26.81$ ,  $df\ 1/96$ ,  $P<0.001$ ). The differences in population growth thus indicate that the non-proportional relationships between the maximum log abundances on ears and leaves were caused by differences in the population dynamics.

For *R. padi*, the relationship remained proportional, with the slope not significantly different from 1 (table 2). This relationship between the numbers of *R. padi* on the leaves and ears (slope=0.69, 95% confidence interval 0.40–1.07) indicated a parallel increase in the numbers on both plant organs, i.e. a symmetrical change in abundance. This was confirmed by the analysis of the population development of *R. padi*, which revealed a density-independent exponential growth on both leaves and ears, i.e. the growth remained unlimited both on ears and leaves.

### Populations of two species on the same plant organ

#### Leaves

On leaves, two-species relationships were investigated by calculating regressions of maximum numbers of *R. padi* or *S. avenae* on those of the dominant species, *M. dirhodum* (fig. 2a–d). The slope of major axis of *R. padi* on *M. dirhodum* (slope=1.42, 95% confidence interval 1.14–1.79) indicated a non-proportional change (table 3). Compared to *R. padi*, *M. dirhodum* became relatively scarce as overall density increased. Both species developed for similar periods of time (one-way ANOVA on day degrees:  $F=1.58$ ,  $df\ 1/108$ , NS). However, the population growth of *R. padi* was not limited, while that of *M. dirhodum* decreased (fig. 4).

In contrast, the slope of the major axis of the relationship of *S. avenae* on *M. dirhodum* (slope=1.01, 95% confidence interval 0.62–1.64) revealed a proportional relationship between maximum abundances of populations of both species. However, in this case the duration of population growth differed between the species. The numbers of *S. avenae* on the leaves increased for a shorter period of time and as a consequence this aphid was less abundant than *M. dirhodum* (one-way ANOVA:  $F=5.40$ ,  $df\ 1/110$ ,  $P=0.02$ ).

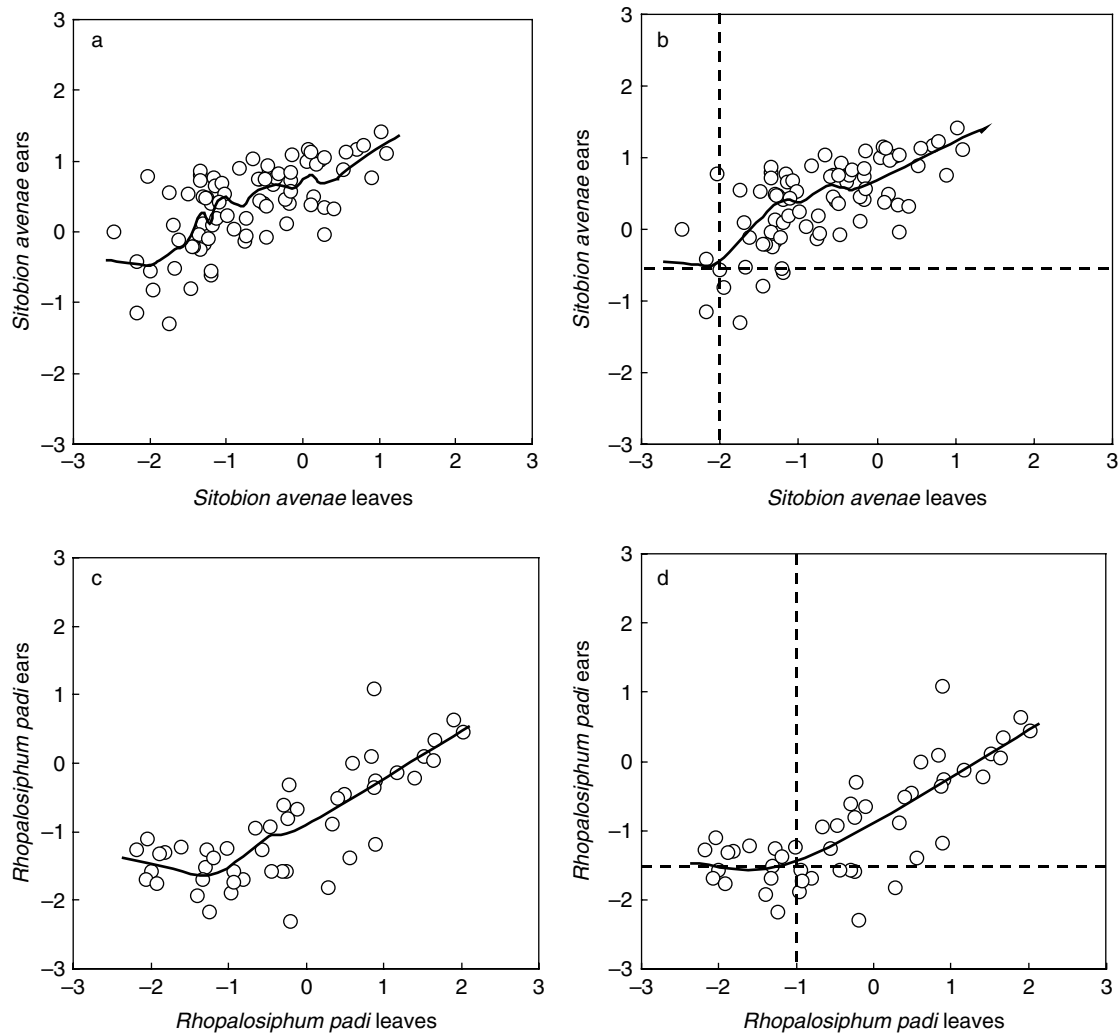


Fig. 1. Logarithmic plots ( $\log_e$ ) of the maxima in the mean number of aphids at the ears vs. that on the leaves (numbers on all leaves and leaf sheaths on a tiller combined). The fitted curves are LOWESS regression models. The regions of effective neutrality, i.e. the regions below which there are no relationships between maximum aphid counts, are indicated by the dotted lines in the right panels. Right and left panels are for the different spans of smoothing that were used to define the region of effective neutrality. a and b: *Sitobion avenae*, the fit of LOWESS regression with span=0.2 and 0.3, region of effective neutrality  $<-2$  (leaves) and  $<-0.5$  (ears); c and d: *Rhopalosiphum padi*, span=0.4 and 0.7, region  $<-1$  (leaves) and  $<-1.5$  (ears).

### Ears

On ears, two-species relationships were investigated by regressing maximum abundances of *R. padi* on *S. avenae* (fig. 2e, f). The slopes of the major axes revealed that the relationships for both species were non-proportional. The slope of major axis was significantly (table 3) greater than 1, for both the data from Praha-Ruzyně (slope=4.55, 95% confidence interval 2.86–10.32) and Sedlec (slope=1.64, 95% confidence interval 1.35–2.03). *Sitobion avenae* and *R. padi* increased in abundance on the ears for the same period of time (one-way ANOVA:  $F=0.95$ ,  $df\ 1/74$ , NS), but *S. avenae* became under-represented as overall aphid density increased (one-way ANOVA:  $F=19.23$ ,  $df\ 1/74$ ,  $P<0.001$ ) (fig. 3).

### Discussion

The present study revealed two patterns in the changes in the proportions of maximum abundance of aphid populations as overall aphid abundance increased. While a proportional relationship (slope of the major axis not significantly different from 1) indicates the absence of constraints on population growth, a non-proportional relationship indicates an asymmetrical constraint, which as the overall density increases, influences one population more than the other. This may result from: (i) inter-specific competition, in which the relative abundance of the competitively inferior species decreases with the increase in abundance of the superior species; (ii) differential changes

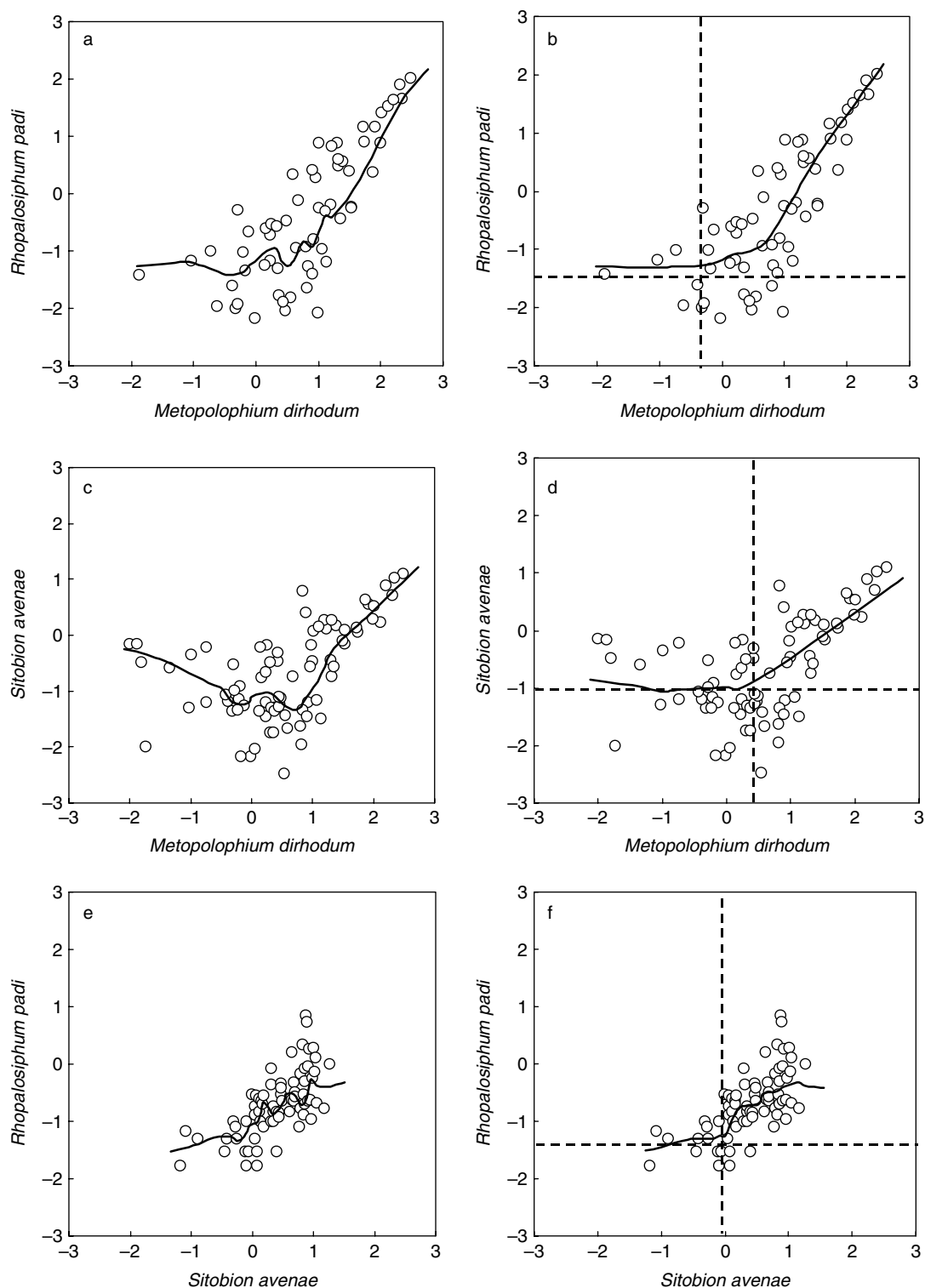


Fig. 2. Logarithmic plot ( $\log_e$ ) of maxima in the mean number of different aphid species on the ears and leaves (all leaves combined as in fig. 1), and their fitted curves and regions of effective neutrality constructed as in fig. 1. a and b: *Rhopalosiphum padi* vs. *Metopolophium dirhodum* on leaves, span of LOWESS regression = 0.2 and 0.4, region of effective neutrality  $< -0.38$  (*M. dirhodum*) and  $< -1.5$  (*R. padi*); c and d: *Sitobion avenae* vs. *M. dirhodum* on leaves, span = 0.5 and 1, region  $< 0.5$  (*M. dirhodum*) and  $< -1$  (*S. avenae*); e and f: *R. padi* vs. *S. avenae* on ears (Sedlec), span = 0.2 and 0.3, region  $< -0.1$  (*S. avenae*) and  $< -1.4$  (*R. padi*).

Table 2. The slopes of major axis (b) and 95% confidence intervals (CI) of the regressions of maximum ln abundance of *Rhopalosiphum padi* and *Sitobion avenae* on ears versus leaves for species that occur on both plant organs.

Species	N	b	CI
<i>S. avenae</i>	69	0.42	0.28–0.60
<i>R. padi</i>	24	0.69	0.40–1.07

N = number of observations. The change in population abundance is proportional if the 95% confidence interval of major axis overlap a slope of 1.

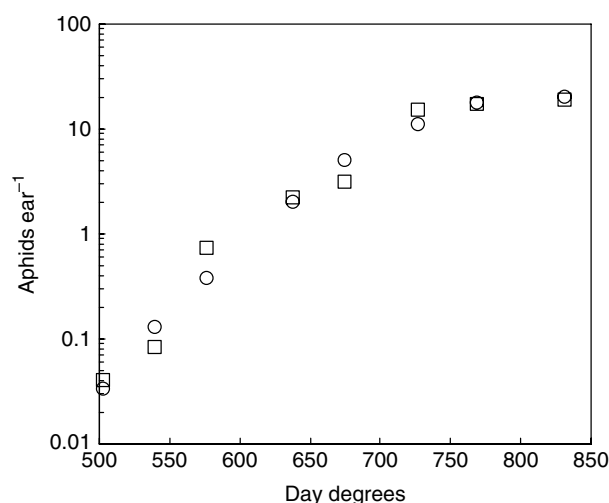


Fig. 3. An example of the curvilinear population growth of *Sitobion avenae* on ears. The population growth decreased in time, expressed in day degrees, as density increased. Fitted values were calculated from the regression model:  $\ln(\text{aphids per ear}) = -37.05 + 0.096 \text{ day degrees} - 0.000057 \text{ day degrees}^2$  ( $F = 303.62$ ,  $df 1/5$ ,  $P = 0.00001$ ,  $R^2 = 98.4\%$ ). An experimental plot at Prague-Ruzyně, 8 June to 7 July, 1992. □, observed; ○, fitted.

in the intensity of intra-specific competition experienced by the two populations as overall population density increases; or (iii) asynchrony in population development (i.e. one species is present for a shorter period of time than the other and the difference increases with aphid abundance). In this study, non-proportional relationships between aphid populations were most likely due to constraints acting upon the more abundant population.

One constraint was a limitation on 'space' for the more abundant species. Living space includes the volume occupied by an animal and the space necessary for feeding, excreting, etc. To fill the 'living space' aphids need not necessarily cover the whole plant surface. Aphid densities per area may be lower, reflecting the trophic and other requirements of particular species. At high aphid abundance, the populations of *S. avenae* grew more slowly on the ears than on the leaves. This non-proportional relationship most likely indicated the existence of a spatial constraint on the ears, because the surface area of ears is smaller than leaves, and the growth of the ear and leaf populations are

Table 3. The slopes of major axis (b) and 95% confidence intervals (CI) of the regressions of maximum ln abundance of *Metopolophium dirhodum*, *Rhopalosiphum padi* and *Sitobion avenae* on leaves and ears.

Species	N	b	CI
Leaves			
<i>R. padi</i> on <i>M. dirhodum</i>	47	1.42	1.14–1.79
<i>S. avenae</i> on <i>M. dirhodum</i>	29	1.01	0.62–1.64
Ears			
<i>R. padi</i> on <i>S. avenae</i> <sup>1</sup>	16	4.55	2.86–10.32
<i>R. padi</i> on <i>S. avenae</i> <sup>2</sup>	56	1.64	1.35–2.03

<sup>1</sup> Praha-Ruzyně, <sup>2</sup> Sedlec.

N = number of observations. The change in population abundance is proportional if the 95% confidence interval of the major axis overlap a slope of 1.

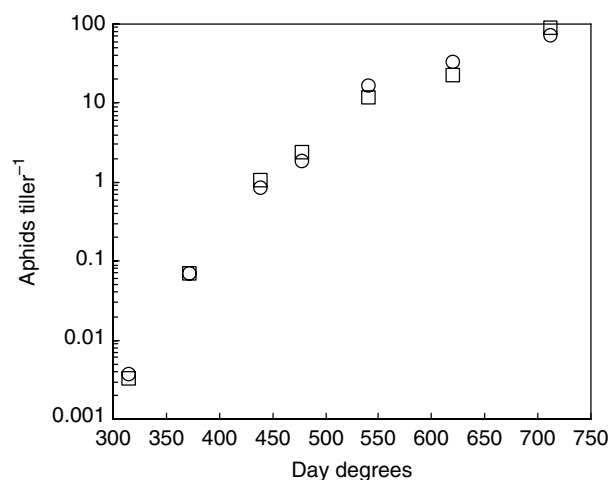


Fig. 4. An example of the curvilinear population growth of *Metopolophium dirhodum* on leaves. The population growth decreased in time, expressed in day degrees, as density increased. Fitted values were calculated from the regression model:  $\ln(\text{aphids per tiller}) = -27.89 + 0.092 \text{ day degrees} - 0.000066 \text{ day degrees}^2$  ( $F = 1035.26$ ,  $df 1/4$ ,  $P = 0.000005$ ,  $R^2 = 99.6\%$ ). An experimental plot at Prague-Ruzyně, 19 May to 27 June, 1989. □, observed; ○, fitted.

likely to be proportional to the available plant surface. An idealized wheat tiller (ear 10 cm long with 60 spherical spikelets 0.5 cm in diameter and a rachis of 0.3 cm diameter, stem 80 cm high with three leaves of 30, 25 and 20 cm<sup>2</sup> area and cylindrical leaf sheaths 0.5 cm in diameter, upper leaf 10 cm below the ear) has a leaf area (260 cm<sup>2</sup>, including outer surface of leaf sheaths) that is about 4.7 times greater than the surface area of the ear (55 cm<sup>2</sup>). Aphid crowding on ears is enhanced by faster population growth of *S. avenae* on the ears than on the leaves (Watt, 1979; Acreman & Dixon, 1989). Although aphids colonize all parts of an ear: spikelet surface, rachis and a section of stem below the ear, the available space may become limiting. This may increase emigration (Holmes, 1988; Chongrattanameteeikul *et al.*, 1991) to leaves of the same or other plants. The higher incidence of predation at the tops of plants, which is typical

for coccinellids and syrphids (Bänsch, 1964; Hodek & Honek, 1996) may also selectively decrease aphid populations on ears.

Similarly, compared to *R. padi*, *M. dirhodum* became relatively scarce on leaves as overall aphid population densities increased, most likely because the populations of *M. dirhodum* are restricted to the leaves, whose area gradually became too small as aphid numbers increased. By contrast, *R. padi* populations were not so constrained. This species is small and colonizes the whole plant. This aphid migrates to other parts, including below-ground stems, and so space is less likely to be a limiting factor. It is a generalist, adapted to cool and humid microclimates (Leather *et al.*, 1989), which does well in dense wheat stands (Honek, 1991a,b). Its unconstrained growth is thus probably a consequence of its tolerance of a wide range of environmental quality and increasing tendency to migrate within and between host plants. The species is also able to populate the inner surfaces of leaf sheaths, where it sometimes becomes more abundant than on leaf blades.

On the other hand, the comparison of the relationship between the numbers of *S. avenae* and *M. dirhodum* on the leaves indicated proportional growth of both species. It is likely that the proportions of the two species remained the same, in spite of the spatial constraints on *M. dirhodum*, due to different durations of population growth, which is shorter in *S. avenae* than in *M. dirhodum*. While *M. dirhodum* remained on the leaves, some of the *S. avenae* moved on to the ears, where they became more abundant than on the leaves. Thus, an increased emigration rate of *S. avenae* from leaves (Holmes, 1988; Chongrattanamateekul *et al.*, 1991) can result in their unconstrained growth on leaves. This migration might be a direct response to the cooler and humid microclimate that prevails on the leaves within a wheat stand. *Sitobion avenae* prefers a warm dry microclimate (Honek, 1985), and its rate of population growth is lower on leaves than ears (Sengonca *et al.*, 1994).

On the ears, the numbers of *S. avenae* and *R. padi* increased for the same period, but *S. avenae* became relatively scarce as overall aphid density increased. This may also have been a consequence of a spatial constraint on the numbers of *S. avenae* on the ears. The numbers of *S. avenae* and *R. padi* increased on the ears for the same period, but *S. avenae* became more abundant than *R. padi* until constrained by the surface area of the ears.

In contrast to spatial limitations operating via intra-specific competition, inter-specific interactions did not seem to influence population growth, at least at the aphid population densities encountered in 1987–1996. The performance of one species in two-species interactions could be explained in terms of the consequences of the spatial constraints acting on that species. On ears, the relative abundance of *R. padi* increased with overall aphid density as a consequence of the spatial constraint on *S. avenae* increase. Similarly on leaves, *R. padi* increased in proportional terms as a consequence of the spatial constraints on *M. dirhodum*. It can also be explained by the biological traits of individual species, like increased rates of population growth of *S. avenae* on ears compared to *R. padi*, and the opposite trend on leaves (Watt, 1979; Acreman & Dixon, 1989).

It is unlikely the differential population growth rates of aphids are influenced by a differential mortality caused by natural enemies. There are no indications of selective

predation on cereal aphids, either by coccinellids (Hodek & Honek, 1996) or other specialist or generalist predators. In the case of polyphagous carabids there are significant preferences for particular aphid species. However, the preferences differ between predator species (Bilde & Toft, 1997) and selective predation is thus unlikely to occur because several carabid species are always present. Moreover, predation by carabids is mainly on aphids dispersing on the ground (Sunderland & Vickerman, 1980; Scheller, 1984; Chiverton, 1988; Winder *et al.*, 1994). Different rates of parasitism have also been recorded (Dean, 1974; Dedryver, 1978; Jones, 1979; Dean *et al.*, 1981). However, parasitoid preferences and rates of parasitization are unlikely to cause systematic differences in species abundance.

It is the abundance of many aphids that makes them such serious pests. Therefore, it is important for aphid pest management to have a good understanding of their population dynamics both in terms of theory and practice. The proposed use of the proportional relationships between the maximum abundances of two aphid species in the field could be useful for detecting differences in the relative growth of aphid populations when overall population density increases. Importantly, the asymmetry in the growth of two co-occurring populations, as revealed by the relationships, was independently confirmed by the density-dependent deviations from exponential growth in one of the co-occurring populations. The analysis of population dynamics thus confirmed the usefulness of the proposed method for detecting constraints on aphid population growth in the field.

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