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The effect of plant quality on the abundance of *Metopolophium dirhodum* (Homoptera: Aphididae) on maize

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Ecology, maize, cereal aphid, population development, abundance, plant growth, stress, dry mass allocation

Abstract. In 1989–1991, populations of *Metopolophium dirhodum* (Walker) on maize in western Czechoslovakia were investigated. Aphid abundance was followed on plants subject to water stress and weed competition and of different ages, sown between late March–late June. Shoot size, growth rate and leaf nitrogen content of the plants affected the performance of aphid populations. Aphids colonized maize stands in early June, after 400 to 500 day degrees (dd), above a 5°C threshold, had accumulated since January 1. Initial abundance varied annually and with host plant size, between 0.1 and 9.9 aphids per plant. Population peak was attained in late June–early July (700–750 dd), after 190–300 dd of exponential population growth. The growth rate of aphid populations was significantly correlated with the growth rate and leaf nitrogen content of maize. Maximum aphid numbers varied annually and were greater on vigorous than on stunted plants. The differences in aphid abundance persisted when recalculated per unit host plant weight. Aphids colonized the lower leaves of maize. The main difference with the population development of *M. dirhodum* on winter wheat was the greater initial numbers per plant. Rate of population growth varied more and its duration was shorter on maize than on wheat. Maximum numbers per unit plant weight were similar on both crops.

INTRODUCTION

There have been several studies on the development of populations of *Metopolophium dirhodum* (Walker) and the factors that determine its maximum abundance on cereals (e.g. Watt, 1979; Cannon, 1985; Zhou et al., 1989; Howard & Dixon, 1990; Honěk, 1991). However, less attention has been paid to the consistently high populations of this aphid that occur on maize each year (Müller, 1961; Hand & Carrillo 1981; Moreau, 1982, 1987; Milinko et al., 1983; Meszaros et al., 1984; Chansigaud et al., 1986; Henry & Dedryver, 1989). Other maize inhabiting species, *Sitobion avenae* (F.), *Rhopalosiphum padi* (L.) and *R. maidis* Fitch, are only abundant in some years (cf. Sakuratani, 1977; Foott, 1977). The factors that determine the maximum abundance of *M. dirhodum* populations on maize have been investigated by Honěk & Martinková (1991) who observed a relationship between host plant quality and aphid population growth rate.

In this study, the development of *M. dirhodum* populations was studied on host plants, which differed either in quality (growth rate and leaf nitrogen content) or age. The results were compared with the parameters of development of *M. dirhodum* populations on winter wheat obtained in an earlier study (Honěk, 1991).

MATERIALS AND METHODS

The development of *M. dirhodum* populations on maize was investigated in 1989–1991. Experiment I was done on a maize crop (cv. CE 330) grown each year at Odolena Voda, about 15 km north of Prague.

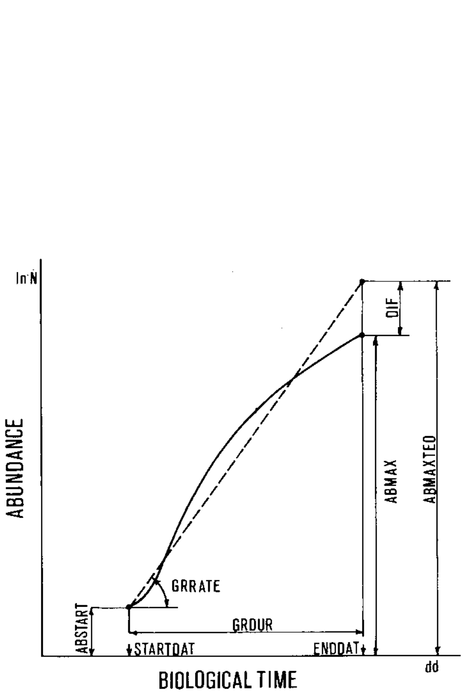

Fig. 1. The model of population growth. Solid line is the development of an aphid population, including an initial acceleration due to immigration, and deceleration at the end due to decreased natality and emigration. Dashed line – the best fit to the *M. dirhodum* data based on a linear regression of all data calculated over the population increase phase. Parameters of population growth are initial abundance, ABSTART, population growth rate, GRRATE, duration of population growth, GRDUR, onset, STARTDAT, and termination of population growth, ENDDAT, fitted, ABMAXTEO, and actual maximum abundance, ABMAX, and their difference, DIF.

The maize crop was sown in late April, and the agricultural practices followed were those accepted in Czechoslovakia, except for the omission of herbicide treatment of some parts of the crop, which permitted the growth of a naturally established stand of a barnyard grass, *Echinochloa crus-galli* (L.) P. Beauv. The density of barnyard grass varied from 20 to 900 plants.m^{-2}. The full soil water capacity, which is correlated with the availability of water for plants (Cassel et al., 1983; Dahiya et al., 1988) ranged from 21.7 to 30.9%. As a consequence, the growth rate and size of individual maize plants at the time of aphid infestation varied due to differences in water availability, caused by variation in soil quality and competition with barnyard grass (Honěk & Martinková, 1991). Every year, the aphid numbers were counted on plants at 3 to 6 sites selected deliberately so that a range of "stunted" and "vigorous" plants were included in the census. Stunted plants had a small growth rate (< 0.010) and nitrogen content (average 2.2% N in dry leaf matter) at the time of peak aphid abundance. Vigorous plants had a high growth rate (> 0.015) and nitrogen content (4.2%). Experiment II was done at Praha – Ruzyně (soil water capacity 30.7%), where cohorts of maize (cv. CE 330) were either sown early, before June 1, or late, after June 1. The sowing dates were April 10, 27, May 12, 29, and June 16, 1989; March 21, April 26, May 7, 16, 25, and June 5, 15, 26, 1990; and May 10, 21, and June 5, 28, 1991. The seeds were sown at 15 cm intervals, in two 5 m rows 1 m apart.

Aphids were counted at weekly intervals, from early immigration until the populations became extinction. At each census the aphids on 20 to 50 plants were counted at each site. The distribution of aphids on 20 plants at each site was recorded at the time of the population peak.

Population growth was modelled (Fig. 1) assuming a linear increase in ln abundance with physiological time, i.e. sum of day degrees (dd). A physiological time scale based on thermal requirements for aphid development was used. The dates were transformed to day degrees above 5°C accumulated from January 1. The value of the lower threshold is the average developmental threshold for aphids (4.1 ± 1.6°C) calculated from data for 28 populations of 16 aphid species (Honěk & Kocourek, 1990). The fitted maximum abundance, ABMAXTEO, is determined by three parameters: initial abundance, ABSTART, duration of population growth, GRDUR and the slope of the linear regression of ln abundance on physiological time (dd) for the period during which the aphids increased in abundance, i.e. the population growth rate GRRATE. ABSTART was the abundance after aphid immigration. GRDUR was time from the onset (STARTDAT) to the termination (ENDDAT) of population growth. Actual population growth rate was usually greater early on, due perhaps to continuing immigration, and smaller later on than the GRRATE calculated over the whole period of aphid population increase. As a result, actual maximum abundance, ABMAX, was usually smaller, by DIF, than the value ABMAXTEO fitted using he average GRRATE.

To determine the growth rate of maize, 5 to 10 plants from each site were harvested 2 to 3 times during the period of aphid population increase and their dry weight determined. Growth rate of maize was the slope of the regression of ln of the weight of the plants on the sum of day degrees above a 10°C threshold

(Martinková, 1989). The nitrogen content of the dry leaves was established by the Kjeldahl method. The water capacity of the soil was determined by submerging in water for 5 days three 50 g soil samples (wrapped in a nylon tissue) from each sample site. The soil was weighed immediately after removal from the water, and when dried to constant weight (at 120°C). The percent water in the soil at full saturation was calculated.

Average daily temperatures were obtained from the meteorological station at Prague Airport, about 3 km from Praha – Ruzyně and 15 km from Odolena Voda.

RESULTS

The parameters of population development

The times of immigration and population peak, duration of population growth, population growth rate and maximum abundance varied between sites and years (Tab. 1 and 2). The first migrants were recorded between May 29–June 8, 1989, May 30–June 14, 1990, and June 12–26, 1991. The date of immigration varied less between stunted and vigorous plants in experiment I than between early and late sown plants in experiment II. In late sown cohorts the STARTDAT was postponed by about 200 dd, and the aphids settled on the 1st true leaf of seedlings a few days after its emergence. The average STARTDAT varied between 512–567 dd, and 403–613 dd in experiments I and II, respectively. Average aphid abundance after immigration ABSTART varied annually with plant quality, between 0.1–9.9 aphids.plant^{-1}. In experiment I, ABSTART (Tab. 1) was correlated with average size of vigorous and stunted plants which was 1.95 and 0.90 g, 2.12 and 0.86 g, and 2.15 and 0.94 g in 1989–1991, respectively. When recalculated per 1 g of dry plant matter, the abundances differed largely in 1989 (6.60 and 3.00 aphids.g^{-1} on vigorous and stunted plants, resp.) and 1991 (1.21 and 0.42 aphids.g^{-1}), but little in 1990 (0.28 and 0.23 aphids.g^{-1}).

The time of population peak, ENDDAT, was little affected by plant quality or sowing date. Annually the ENDDAT varied by 1 week (or 100 dd). The decline in aphid abundance was not associated with the senescence of the plants. Maize continued to grow even after the aphid population peaked. Eventually, aphid population growth also ceased (in mid-July) also on the young plants of experiment II, sown as late as June 26, < 50 dd later than on the early sown plants. The duration of aphid population growth, GRDUR, was slightly longer on vigorous than on stunted plants of experiment I, but much longer on early than on late sown cohorts of experiment II.

The growth rate, GRRATE, of aphid populations in experiment I was lower on stunted than on vigorous plants (see 3.2) and in experiment II lower on late than on early sown plants. The differences were similar each year.

The peak number of aphids per plant, ABMAX, varied greatly between years even on plants of similar quality (by a factor of 10–30). It also varied within years on plants of different quality (by 20–200 in experiment I, and 5–10 in experiment II). Aphid numbers per plant increased with plant size. Nevertheless, the size of a host plant did not limit aphid population growth. The differences in experiment I persisted after the aphid numbers were recalculated per unit dry shoot weight, when the abundances on stunted and vigorous plants differed by a factor of 8 to 26. The recalculated values of abundance on early and late sown plants of experiment II did not differ.

TABLE 1. Aphid population growth on stunted (S) and vigorous (V) plants of maize, experiment I. N = number of samples, GRAT = growth rate and SWT = dry shoot weight at the time of maximum aphid abundance. The parameters of the growth of *M. dirhodum* populations are those given in Fig. 1 plus maximum abundance per g dry shoot weight (GMAX). Average ± SE, ABMAX and GMAX in non-logarithmic form.

		N	Maize		*Metopolophium dirhodum*						
			GRAT	SWT	STARTDAT	ENDDAT	GRDUR	ABSTART	GRRATE	ABMAX	GMAX
1989	S	1	0.0097 —	3.1 —	491 —	720 —	229 —	2.7 —	0.0027 —	6.2 —	2.0 —
	V	2	0.0155 ±2.0E-4	22.5 ±5.85	478 ±13.4	720 ±0	242 ±13.4	9.9 ±1.98	0.0193 ±7.0E-4	1714.7 ±1.1E+3	67.9 ±29.2
1990	S	2	0.0059 ±5.0E-4	2.3 ±0.75	621 ±19.0	799 ±27.5	178 ±4.6	0.2 ±0.10	0.0037 ±1.7E-4	0.7 ±0.0	0.4 ±0.11
	V	3	0.0120 ±1.1E-3	14.4 ±9.74	585 ±24.5	808 ±25.9	223 ±1.9	0.6 ±0.02	0.0152 ±6.5E-3	84.7 ±95.4	3.3 ±1.67
1991	S	1	0.0076 —	2.8 —	536 —	696 —	160 —	0.4 —	0.0054 —	3.9 —	1.5 —
	V	4	0.0126 ±4.5E-4	10.9 ±5.02	474 ±23.0	696 ±0.0	222 ±23.0	2.6 ±0.70	0.0203 ±4.1E-3	72.7 ±52.5	21.4 ±11.7
MEAN	S	4	0.0071 ±7.8E-4	2.6 ±0.17	567 ±33.3	753 ±28.7	186 ±14.0	0.9 ±0.61	0.004 ±5.2E-4	2.9 ±1.3	1.1 ±0.41
	V	9	0.013 ±5.5E-4	14.7 ±2.21	512 ±19.8	739 ±18.3	227 ±6.5	3.5 ±1.36	0.0185 ±1.9E-5	441.6 ±300.6	25.7 ±10.14

TABLE 2. Aphid population growth on early sown (E, March–May) and late sown (L, June) cohorts of maize plants, experiment II. Symbols and explanations as in Table 1.

		N	Maize		*Metopolophium dirhodum*						
			GRAT	SWT	STARTDAT	ENDDAT	GRDUR	ABSTART	GRRATE	ABMAX	GMAX
1989	E	3	— —	— —	477 ±0.0	739 ±0.0	262 ±0.0	0.8 ±0.39	0.0288 ±3.5E-3	739.9 ±54.8	— —
	L	2	— —	— —	611 ±42.0	739 ±0.0	128 ±42.0	0.9 ±0.14	0.0374 ±2.5E-3	152.3 ±121.3	— —
1990	E	5	0.0145 ±1.7E-3	23.1 ±6.10	338 ±30.1	675 ±7.8	337 ±34.9	0.1 ±0.03	0.0248 ±2.6E-3	302.3 ±57.8	17.5 ±3.91
	L	3	0.0145 ±6.0E	1.2 ±0.71	582 ±43.3	677 ±10.7	95 ±44.9	0.3 ±0.16	0.0477 ±1.3E-2	34 ±23.3	22 ±4.03
1991	E	2	0.0173 ±2.9E-4	10.4 ±0.95	454 ±0.0	712 ±0.0	258 ±0.0	0.1 ±0.01	0.0239 ±8.0E-3	31.1 ±8.40	3.1 ±0.78
	L	2	0.0141 ±0.0	1.0 ±0.65	663 ±49.5	758 ±45.5	95 ±4.0	0.1 ±0.09	0.0324 ±2.4E-2	5.7 ±5.30	3.8 ±0.28
MEAN	E	10	0.0153 ±1.8E-3	19.5 ±4.49	403 ±26.0	702 ±10.1	299 ±20.8	0.3 ±0.15	0.0258 ±1.7E-3	379.3 ±91.1	13.4 ±3.73
	L	7	0.0143 ±3.2E-4	1.2 ±0.40	613 ±25.6	718 ±18.1	105 ±20.3	0.4 ±0.14	0.0404 ±7.8E-3	59.7 ±37.1	14.7 ±4.73

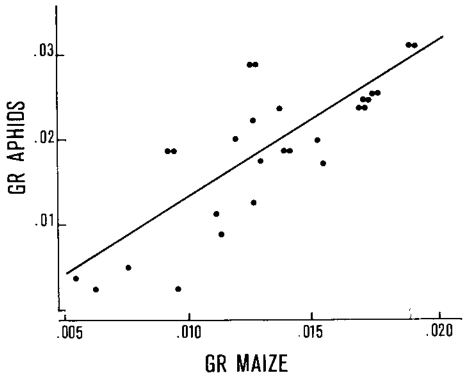

Fig. 2. Growth rate (GR) of maize plants during the period of aphid infestation, and growth rate of the aphid populations (GRRATE). Combined data from experiment I and early sown plants of experiment II, in 1989–1991. Regression: GRRATE = 1.83 maize growth rate – 0.005; $r = 0.807$, $p < 0.001$.

Plant quality and the growth rate of aphid populations

The average growth rate of aphid populations, GRRATE, was directly proportional ($r = 0.807$, $p < 0.001$) to the growth rate of maize (Fig. 2), and to the nitrogen content of the leaves (Fig. 3). On the late sown plants of experiment II the growth rate was higher than on the early sown plants. Immigration perhaps continued throughout the whole short period of aphid population growth on the late sown plants and increased the GRRATE.

Maximum aphid abundance

The factors determining maximum abundance (Fig. 1) were analysed separately for the combined data of experiment I and early sown cohorts of experiment II (Fig. 4). In experiment I, the fitted maximum abundance, ABMAXTEO, was significantly correlated with the growth rate of aphid populations, GRRATE, ($r = 0.903$), initial abundance, ABSTART, ($r = 0.815$), and duration of population growth period, GRDUR, ($r = 0.761$). There was a high inter-correlation between these parameters. The time of aphid immigration, STARTDAT, largely determined the GRDUR ($r = -0.542$). The difference, DIF, between fitted ABMAXTEO and actual ABMAX on vigorous plants of experiment I was –0.838 ln aphid number.plant^{-1}. On stunted plants DIF varied around zero, with an average

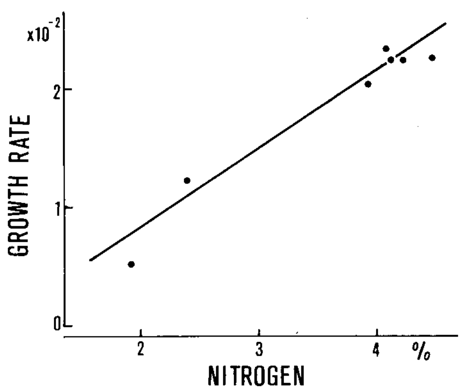

Fig. 3. Nitrogen content of maize leaves (% of dry matter, June 26) and growth rate (GRRATE) of aphid populations. Combined 1991 data from experiment I and early sown plants of experiment II. Regression: GRRATE = 7.22E-3 N percent – 6.46E-3; $r = 0.970$, $p < 0.001$.

value of + 0.303. In experiment II ABMAXTEO was significantly affected by ABSTART, which varied annually and with plant size (age). The effect of GRRATE and GRDUR was smaller. The DIF for early sown plants was small (–0.094).

Distribution of aphid populations on plants

At the time of the population peak most aphids were on the lower leaves, 2nd–4th leaf from the bottom of stunted plants, and 3rd–6th leaf of vigorous plants in experiment I (Fig. 5). The upper leaves were free of *M. dirhodum*. However, on July 5, 1989 the nitrogen content of the lower leaves (3.73%) and upper leaves (3.33%) of plants of experiment II sown on April 27, differed little. This difference was small compared to difference in the N content of stunted and vigorous plants of experiment I (Fig. 3, Tab. 3), and may not be the factor determining aphid distribution.

TABLE 3. The parameters (average ± SE) of development of *M. dirhodum* populations on stunted and vigorous maize (M) and winter wheat (W) plants. Symbols as in Table 1, ABSTART, ABMAX, and GMAX in non-logarithmic form.

Parameter	Crop	Host plant	
		Stunted	Vigorous
STARTDAT	W	555±41	311±20
	M	567±33	455±23
ENDDAT	W	709±13	690±4
	M	753±29	720±14
GRDUR	W	154±23	380±20
	M	186±14	265±14
ABSTART	W	0.08±0.02	0.02±0.01
	M	0.9±0.6	1.8±0.7
GRRATE	W	0.0255±0.0046	0.0288±0.0014
	M	0.0040±0.0005	0.0223±0.0009
ABMAX	W	0.8±0.7	107.6±16.7
	M	2.9±1.3	408.8±190.3
GMAX	W	0.9±0.6	42.4±11.8
	M	1.1±0.4	19.2±6.8
Leaf nitrogen (%)	W	1.98	3.95
	M	2.18	4.16

DISCUSSION

A comparison of the performance of *M. dirhodum* on maize and winter wheat

Reproduction, ontogeny and abundance of insect species may be affected by the photosynthetic pathways of the host plant (Caswell et al., 1973; Capinera, 1978; Pinder & Kroh, 1987). It is therefore interesting to compare the parameters of population growth of *M. dirhodum* on maize, which has a C_4 photosynthetic pathway, and winter wheat, a C_3 plant. *M. dirhodum* performance on stunted and vigorous maize plants was compared with that on stunted sparse (SPA) and vigorous solitary (SOL) plants of winter wheat (Honěk, 1991). Solitary wheat plants were selected for comparison since they experience similar ambient conditions to sparsely planted maize plants. It should be mentioned, however, that aphid

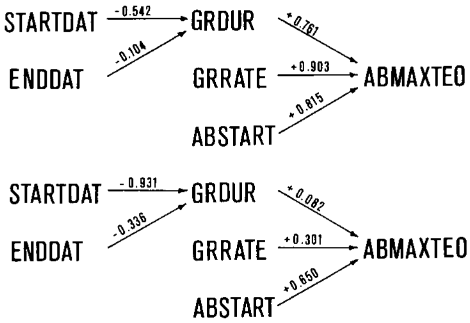

Fig. 4. The correlations between fitted maximum abundance, ABMAXTEO, and its determinants, initial abundance, ABSTART, duration of population growth, GRDUR, population growth rate, GRRATE, time of the onset of population growth, STARTDAT, and time of the termination of population growth, ENDDAT. Above: Experiment I, 1989–1991, below: early sown plants of experiment II, 1989–1991 data.

numbers on SOL wheat plants are much greater than on plants of ordinary densely planted wheat crops.

Initial abundance was 12 and 82 times greater on stunted and vigorous maize plants than on the respective wheat plants. This was the most important difference between maize and wheat. It may be due to differences in planting density; the recommended planting density for maize is 7 plants.m^{-2} and wheat ca. 400 tillers.m^{-2}. The immigrant aphid population is thus "diluted" over many wheat plants and a few maize plants. Similar numbers of immigrant aphids colonized wheat, ca. 8 aphids.m^{-2}, and maize, ca. 14 aphids.m^{-2}. A preference for alighting on large plants (cf. Ahman et al., 1985; Antolin & Addicot, 1991) could also increase numbers of aphids on maize as the aphids may prefer stands consisting of large plants. The vigorous wheat crops had an earlier STARTDAT (by 114 dd), and longer GRDUR (by 115 dd) than vigorous maize crops. GRRATE of stunted plants was greater for wheat, by a facor of 6, while for vigorous plants it was essentially similar in both crops. The average maximum aphid numbers per plant (or tiller) were 3.6 to 3.8 times greater on maize than on wheat. The main cause of this difference was the initial aphid number per plant. When the numbers of aphids are expressed per unit shoot weight, the difference in maximum abundance was very small for stunted plants, and for vigorous plants the abundance was even greater on wheat than on maize.

Growth of populations could be probably affected also by plastic ontogenetic adaptation to changing environment conditions which is typical for aphids. It includes a change of aphid size and development time which tends to optimize aphid population response to environment conditions (Kindlmann & Dixon, 1989; 1992).

Factors of vertical distribution of aphids

The vertical distribution of aphids on maize is similar as in western Europe (Henry & Dedryver, 1989) and apparently not caused by local climate. The vertical distribution on maize differed from that on wheat (Fig. 5). Some host plant characters vary in parallel, e.g. the density of stomata (Fitter & Hay, 1987) is greater on lower than at the upper leaves of maize, while the reverse is true for wheat. The morphological differences may parallel differences in host plant metabolism, which affect aphid feeding. The main cause of the differences in aphid performance may be the intensity of assimilate production and/or transport, which are affected by leaf age and the proximity of sinks. In wheat, the most

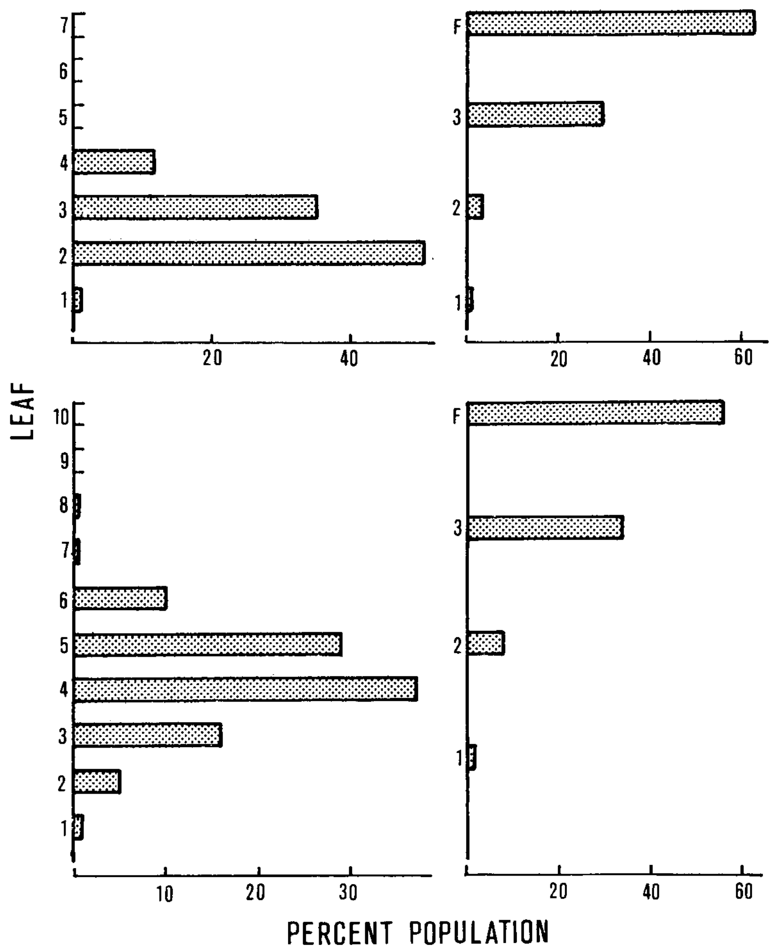

Fig. 5. The distribution of *M. dirhodum* on maize (left, at the time of the population peak in experiment I, 1991) and winter wheat (right, "aphid load" from Honěk, 1991). The bars indicate the proportion of the population of *M. dirhodum* present on different leaves. The leaves are numbered in order from the ground, F – flag leaf. Above: stunted maize plants, or "sparse" wheat plants. Below: vigorous maize plants, or "solitary" wheat plants.

intense production occurs in the flag leaf, which transports assimilates to the ear (Rawson et al., 1983). In maize, the rate of photosynthetic activity increases up to full leaf expansion and then decreases. It is also greater and persists longer in the leaves near to the growing cobs (Dwyer et al., 1989). In fact, *M. dirhodum* populations are greater on lower leaves, which have just finished their growth and are near to the lower cobs. As a consequence, the vertical distribution of *M. dirhodum* is plastic and may probably vary also with minor differences among host crop cultivars. Thus, in northern France, the distribution on winter wheat (Dedryver, 1978) differed from that observed in the Czech Republic (Honěk, 1991).

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