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Karyotype variation in the corn leaf aphid, *Rhopalosiphum maidis* (Fitch), species complex (Hemiptera: Aphididae) in relation to host-plant and morphology

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Abstract

Rhopalosiphum maidis (Fitch) collected on barley in the northern hemisphere usually has a ten-chromosome karyotype, whereas samples from maize, sorghum and Johnson grass (*Sorghum halepense*) from all parts of the world commonly have $2n = 8$. Samples with other karyotypes ($2n = 9$, $2n = 11$ and $2n = 8$ heterozygous for an interchange between the X chromosomes) occur less frequently on these and other species of Gramineae. Multivariate morphometric analysis, principally by the method of canonical variates, indicated that the ten-chromosome form may be regarded as a single clone of *R. maidis* recognizable by its karyotype and host-plant relationships, although not completely separable by morphology alone from all other clones of this permanently parthenogenetic species complex.

Introduction

The corn leaf aphid, *Rhopalosiphum maidis* (Fitch), is a pest of cereal crops throughout the world, transmitting viruses of barley, maize and sorghum. All populations seem to be entirely parthenogenetic; males are occasionally recorded, but in species of the genus *Rhopalosiphum* a functional sexual phase would probably involve migration to a woody, rosaceous primary host-plant, and there is no evidence that this occurs in *R. maidis* anywhere in the world. Populations of *R. maidis* therefore comprise an indefinable number of separate parthenogenetic lineages. Five of these lineages were isolated by workers in Kansas, USA, and described as 'biotypes', characterized mainly by their differing abilities to colonize varieties of barley and sorghum (Painter & Pathak, 1962; Wilde & Feese, 1973). It is not known whether these same biotypes are recognizable in other parts of the USA, or in other parts of the world. Steiner *et al.* (1985) found enzyme (esterase) differences between *R. maidis* samples collected in northern and southern USA.

Differences in karyotype between samples of *R. maidis* have been reported (Blackman & Eastop, 1984; Chattopadhay *et al.*, 1982). Preliminary studies of samples of *R. maidis* from various parts of the world provided evidence that certain karyotypes may be correlated with particular host-plant relationships and morphological characters, and this might lead to the recognition of separate taxonomic entities within the *R. maidis* complex on a worldwide basis (Blackman *et al.*, 1987).

In this paper, we analyse the different karyotypes of *R. maidis* in more detail and present results of a multivariate morphometric study of samples from all parts of the world.

We also examine the correlations between the karyotype and the morphology of a sample and the host-plant on which it was collected, and discuss their taxonomic significance.

Materials and methods

The karyotyped material comprised 110 samples of *R. maidis* from 18 countries in six continents (Table I). Aphids were preserved in 3:1 methanol:acetic acid. Embryos were dissected from two or three, usually immature, specimens of each sample, hydrolysed in hydrochloric acid and squashed in 45% propionic acid (see Blackman (1980) for details of method). Somatic cell nuclei in prometaphase or metaphase stages were photographed and the negative images projected onto graph paper in order to measure the relative lengths of individual chromosomes.

TABLE I. *Samples of* Rhopalosiphum maidis *karyotyped and/or measured*

Sample no.	No. of chromosomes	Host-plant	Locality	No. of measured specimens	
				Apterae	Alatae
1234	9*	"Grass"	New South Wales	5	—
1241	8	Sorghum	California	8	6
1541	8	Wheat	Iran	—	—
1977	8	?	Ivory Coast	—	4
2117	8*	Johnson grass	Portugal	5	7
2350	8	*Avena sterilis*	Portugal	10	—
2359	10	Barley	Montana	12	11
2361	10	Barley	Montana	13	8
250101	10	Barley (ex cult. 25°C, 16-h day)	England	24	23
250102	10	Barley (ex cult. 20°C, 16-h day)	England	23	21
250103	10	Barley (ex cult. 16°C, 12-h day)	England	24	23
250104	10	Barley (ex cult. 10°C, 12-h day)	England	19	24
250105	10	Barley (ex cult. 30°C, 16-h day)	England	24	24
2582	8	Maize	Botswana	7	14
2584	9*	Barley	Iran	—	—
2588	8*	Maize	Iran	29	—
2621	9*	"Grass"	Israel	—	—
2663	9*	Johnson grass	Uruguay	—	—
2677	8	Sorghum	Israel	—	—
2678	8	Sorghum	Israel	8	—
2684	10	Oat	Cyprus	—	—
2766	10	Barley	Quebec	14	9
2767	8	Barley (ex cult.)	Ontario	38	14
2792	8*	Sorghum	Israel	5	—
2809	11*	Maize	Iran	14	8
2814	8	Maize	Iran	12	4
2817	9*	Wheat	Iran	15	—
2829	8	Johnson grass	Uruguay	—	—
2834	8	Sorghum	Iran	—	—
2835	10	*Setaria viridis*	Iran	13	—
2836	8	Johnson grass	Iran	25	—
2839	8	Wheat	Jordan	—	—
2922	9*	*Echinochloa crus-galli*	Iran	13	—
2923	8	*Echinochloa crus-galli*	Iran	21	—
2924	8	Johnson grass	Iran	—	—
2925	9*	*Echinochloa crus-galli*	Iran	12	—
2944	8	*Echinochloa crus-galli*	Iran	—	—
2945	8	Maize or sorghum	Iran	—	—
2946	8	Maize	Iran	—	—
2949	8	Maize	Iran	20	5
3018	9*	*Pseudosasa japonica*?	New Zealand	—	—
3231	8	Maize	Tasmania	9	5
3274	9*	*Echinochloa crus-galli*	Tasmania	12	22
3307	8	Barley (ex cult.)	New York	19	—
3339	10	Barley	Washington	24	—
3489	8	Maize	Ohio	—	—
3490	8	Sorghum	Japan	12	—
3491	8	Sorghum	Japan	—	—
3492	8	Maize	Ohio	24	12
3507	8	Maize	Egypt	12	—
3508	8	Sorghum	Japan	13	12
3510	8	Maize	Egypt	13	—
3511	8	Maize	Egypt	12	—

Sample no.	No. of chromosomes	Host-plant	Locality	No. of measured specimens: Apterae	Alatae
3512–3	8	Maize (2 samples)	Egypt	—	—
3522	8	Barley	Tasmania	11	12
3523–6	8	Maize (4 samples)	Idaho	12	12
3527	8&10	Maize	Idaho	12	12
3528	8	Maize	Idaho	12	12
3529–31	10	*Echinochloa crus-galli* (3 samp.)	Idaho	12	12
3532	10	*Setaria pumila*	Idaho	12	12
3533	10	*Panicum capillare*	Idaho	12	12
3542	8	Barley	Kansas	12	—
3543	8	Johnson grass	Georgia	—	12
3544	9*	Johnson grass	Georgia	11	9
3545	8	"Grass"	Texas	—	—
3546	8	Johnson grass	Texas	—	—
3547	9*	*Setaria* sp.	Texas	13	12
3548	8	Johnson grass	Mississippi	12	—
3549	8	*Setaria* sp.	Illinois	12	—
3550	8	Johnson grass	Alabama	—	—
3551	8	Johnson grass	Texas	—	—
3552	8	Maize	Peru	12	—
3553	8	Johnson grass	Alabama	13	—
3554	8	Johnson grass	Oklahoma	12	12
3555	8	Johnson grass	Texas	12	—
3556	8	Johnson grass	Arkansas	—	—
3557	8	Johnson grass	Texas	12	—
3558–60	8	Maize (3 samples)	Montana	—	12
3561–70	10	Barley (10 samples)	Montana	—	12
3572	8	Johnson grass	Texas	10	12
3573	8	Maize	Quebec	—	—
3575	8	Johnson grass	Georgia	12	9
3576	8	Johnson grass	Alabama	12	12
3578	8	Sorghum	Texas	12	—
3579	8	Johnson grass	Illinois	—	—
3581	9*	Sorghum	Texas	12	—
3583	8	Johnson grass	Louisiana	12	12
3602	8	Johnson grass	Israel	11	12
3607	8	Maize	Israel	—	—
3619	9*	*Bromus catharticus*	Israel	—	—
3629	8	Johnson grass	USA	12	—
3701	8	Barley	South Africa	—	12
3702	8	Maize	South Africa	—	12
KS-1	—	Barley (ex cult.)	Kansas	19	20
KS-2	—	Barley (ex cult.)	Kansas	12	7
KS-3	—	Barley (ex cult.)	Kansas	14	17
KS-4	—	Barley (ex cult.)	Kansas	13	8

* Heterozygous karyotype.

The material for morphometric study comprised 70 samples of adult apterous virginoparae and 60 samples of adult alate virginoparae. Aphids prepared specifically for this work were macerated, cleared and mounted in Canada balsam using Martin's method (Martin, 1983). Samples of the four 'biotypes' of Painter & Pathak (1962), already available on slides in the British Museum (Natural History) collection, were also measured. Measurements were made according to the methods illustrated in Ilharco & van Harten (1987), except that body length was measured from the front of the head to the end of the eighth abdominal tergite rather than to the end of the cauda.

At least four and usually 12 specimens were measured for multivariate analysis. A preliminary study was made of the correlations between 32 characters for 11 samples. Ten of these characters were selected for the full analysis (Table II). The selected characters were relatively easy to measure, had comparatively low coefficients of correlation with one another and were considered most likely to be discriminatory on the basis of previous experience with the group. For alatae, counts of the numbers of secondary sensoria (rhinaria) on antennal segments 3, 4 and 5 were also included in the analysis (apterae do not have these sensoria).

One clone with the ten-chromosome karyotype was reared on barley for more than three generations in controlled environmental conditions at five different temperatures (10, 16, 20, 25 and 30°C) in order to determine the effect of this one environmental variable on

TABLE II. *Morphological characters of* Rhopalosiphum maidis *measured for biometric analyses*

1. Body length (exclusive of cauda).
2. Length of antennal segment 3 (AS3).
3. Length of antennal segment 4 (AS4).
4. Length of antennal segment 5 (AS5).
5. Length of base of antennal segement (AS6 base).
6. Length of terminal process of antenna (AS6 PT).
7. Length of ultimate rostral segment (URS).
8. Length of hind tarsal segment (HT2).
9. Length of siphunculus.
10. Length of cauda.
11. Number of secondary rhinaria on antennal segment 3 (alatae only).
12. Number of secondary rhinaria on antennal segment 4 (alatae only).
13. Number of secondary rhinaria on antennal segment 5 (alatae only).

TABLE III. *Relative length data for different karyotypes of* Rhopalosiphum maidis, *pairing presumed homologues*

	Karyotype			
Chromosome	$2n = 8$ (homozygous)	$2n = 10$	$2n = 9$	$2n = 8$ (heterozygous)
X	12·18 12·18	12·37 12·37	12·70 12·70	X_L 20·39, X_S 5·14 $\frac{X_L + X_S}{2} = 12{\cdot}77$
A1	15·45 15·45	15·67 9·18 + 6·34 = 15·52	15·70 15·70	15·24 15·24
A2	14·00 14·00	13·87 7·21 + 6·85 = 14·06	14·24 6·51 + 5·69 = 12·20	13·45 13·45
A3	8·35 8·35	8·11 8·11	8·33 8·33	8·55 8·55
No. of chromosome sets measured	105	34	49	12

morphology and to assess the extent of potential morphological variation within clones. No other clones of *R. maidis* were reared, so there was no possibility of contamination with this genotype.

The morphometric data, comprising a total of 17 332 measurements on 1709 individual specimens, were analysed on a PDP computer using the methods of principal components and canonical variates.

Results

Karyotypes

Five different karyotypes were recognized. Four of these are illustrated in Fig. 1, and relative length data are given in Table III. The data are arranged in a way that enables some comparison between karyotypes, although it was not possible to test these comparisons statistically in any meaningful way because of the unquantifiable errors in the measuring and ranking procedure. The commonest and most widespread karyotype consisted of eight chromosomes (Fig. 1*a*), with relative length measurements indicating that the component elements could be matched in pairs (Table III); that is, this karyotype seemed to be structurally homozygous. Relative length values for six clones of this karyotype were calculated separately; no significant differences were found between clones. X chromosomes could not be definitely identified as no male embryos were available, but the third largest

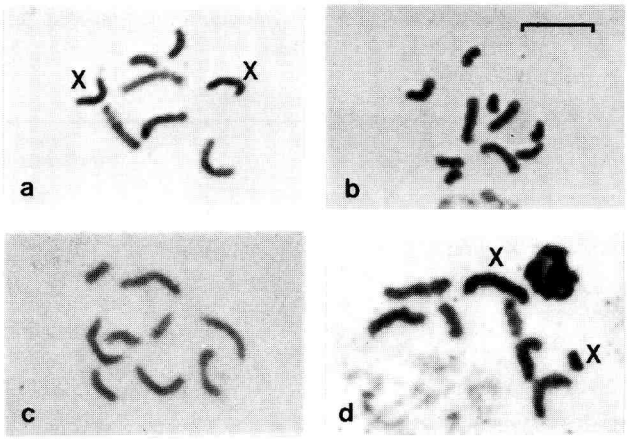

Fig. 1.—Somatic prometaphase chromosome sets of *Rhopalosiphum maidis*: (*a*) $2n = 8$ (homozygous), (*b*) $2n = 10$, (*c*) $2n = 9$ and (*d*) $2n = 8$ (heterozygous). (Putative X chromosomes marked 'X'. Scale bar represents 5 μm.)

pair tended to condense earlier than the others and often had nucleoli associated with them in early prophase; both these properties are reliable indicators that this pair were the X chromosomes. This karyotype is very like that of *R. padi* (L.) and *R. rufiabdominalis* (Sasaki).

Aphids with this karyotype came from all continents and were particularly found on Johnson grass (*Sorghum halepense*), sorghum (*S. bicolor*) and maize, although samples were also obtained from wheat, oats, *Echinochloa crus-galli* and *Setaria* spp. Only two samples were known to be collected from barley (one from South Africa and the other from Egypt), although the eight-chromosome form can be maintained on barley in the laboratory.

A ten-chromosome karyotype was also common (Fig. 1*b*). Initially, it was thought to be structurally homozygous with five matching pairs of chromosomes similar to that of *R. insertum* (Walker). However, when relative length data were analysed (Table III), it was found that the ten-chromosome form could best be derived from the eight-chromosome karyotype by dissociation of two, non-homologous autosomes. Aphids with the ten-chromosome karyotype have so far been obtained only from the northern hemisphere, where they are the normal form on barley and also occur on oats, *Panicum capillare*, *E. crus-galli* and *Setaria* spp. but not on *Sorghum* spp. or maize.

Three other karyotypes were far less common. Aphids with nine chromosomes in somatic cell nuclei (Fig. 1*c*) were collected in the Middle East (eight times), Australasia (three times), North America (three times) and South America (once). They came from barley, Johnson grass, sorghum, wheat, *E. crus-galli*, *Arundinaria* sp. and unidentified grasses. Relative length data did not agree very well with the simplest hypothesis of an autosome 2 dissociation (Table III), so some more complex change may have occurred. A fourth karyotype, found in samples from Portugal, Iran and Israel, had eight chromosomes but was structurally heterozygous. Observations suggested an unequal interchange between the two X chromosomes, and this was supported by the relative length data (Table III). The fifth karyotype, with 11 chromosomes, has only been found once, on maize in Iran, and insufficient dividing cells were available for any quantitative analysis.

Association between karyotype and host-plant

Samples are grouped according to karyotype and host-plant in Table IV. The association of $2n = 8$ (homozygous) samples with *Sorghum* spp. and maize, and of $2n = 10$ samples

TABLE IV. *Associations between karyotype and host-plant in* Rhopalosiphum maidis

Host-plant	Karyotype				Totals
	$2n = 8$ (homozygous)	$2n = 10$	$2n = 9$	$2n = 8$ (heterozygous)	
Maize	24 (15·2)	0 (5·7)	0 (3·4)	1 (0·8)	25
Sorghum spp.	28 (20·1)	0 (7·5)	3 (4·4)	2 (1·0)	33
Barley	2 (10·9)	15 (4·1)	1 (2·4)	0 (0·6)	18
Echinochloa crus-galli	1 (4·3)	3 (1·6)	3 (0·9)	0 (0·2)	7
Other Gramineae	4 (8·5)	4 (3·2)	6 (1·9)	0 (0·4)	14
Totals	59	22	13	3	97

Numbers in brackets are expected values on the basis of no association.

with barley + other Gramineae, is highly significant ($\chi^2 = 53{\cdot}9$, 2 d.f., $P < 0{\cdot}001$). Not enough samples of the other karyotypes were available for statistical tests of association.

Morphometrics

When all specimens were grouped according to karyotype, comparisons of the overall means of the ten characters measured revealed certain differences (Table V). Specimens from the ten samples with $2n = 9$ were significantly smaller in all measurements than the corresponding morphs with eight and ten chromosomes. Apterae with the heterozygous eight-chromosome karyotype were significantly larger than those of other karyotypes, but as they all came from a single sample this could be a matter of chance. The principal comparison in Table V is between ten-chromosome aphids and those homozygous for $2n = 8$, where the number of samples involved is large enough to compensate for between-sample differences in general body size. Mean body length was the same for these two karyotypes in both apterae and alatae, so it is possible to compare other characters to some extent without regard to the effects of general size. Both apterae and alatae of the ten-chromosome form have a longer antennal terminal process, a longer third antennal segment and a shorter second hind tarsal segment, than the corresponding morphs with $2n = 8$. In the alatae, the fifth antennal segment and the ultimate rostral segment are also longer, and the cauda is shorter.

Bivariate plots illustrate some of the differences between eight- and ten-chromosome apterae (Figs 2 & 3) and alatae (Figs 4 & 5), and also show the distributions of values for individual specimens. The classification into karyotype is based on only a few individuals from each sample, so it is possible that some of the points represent misclassifications. A ten-chromosome individual was in fact found in one $2n = 8$ sample from maize in Idaho, and although that sample was excluded from the morphometric study, some of the anomalous points in Figs 2–5 could be due to similar but undetected 'contamination' of other samples with individuals of the other karyotype. The morphological distinction between the eight- and ten-chromosome samples in these bivariate plots may therefore be somewhat underestimated.

Principle component analysis.—Principal components analysis was carried out on a reduced, standardized data set to examine the extent of variation within samples, particularly where there was a suspicion that a sample might contain individuals of more than one karyotype. The reduced data set for both apterae and alatae comprised 21 samples, each of ten specimens, and in the case of each morph included the seven 'most suspect' samples, plus seven samples selected on the basis of preliminary study as safely attributable to each karyotype, either because they were laboratory clones or because the mean values of all

TABLE V. *Overall means and standard deviations for measurements of ten morphometric characters of different karyotypes of* Rhopalosiphum maidis

APTERAE	$2n = 10$ Mean	s.d.	$2n = 8$ (homozygous) Mean	s.d.	$2n = 8$ (heterozygous) Mean	s.d.	$2n = 9$ Mean	s.d.
Body length	1·72^{ns}	0·28	1·68^{ns}	0·41	1·98	0·21	1·46	0·38
AS3†	0·181***	0·040	0·163***	0·045	0·200	0·031	0·136	0·052
AS4	0·100^{ns}	0·21	0·097^{ns}	0·022	0·116	0·017	0·082	0·025
AS5	0·097^{ns}	0·019	0·094^{ns}	0·020	0·105	0·010	0·079	0·021
AS6 base	0·083^{ns}	0·012	0·082^{ns}	0·011	0·088	0·006	0·073	0·011
AS6 PT	0·191***	0·025	0·167***	0·024	0·174	0·011	0·151	0·027
URS	0·086^{ns}	0·006	0·085^{ns}	0·009	0·090	0·005	0·080	0·013
HT2	0·096**	0·009	0·098**	0·012	0·108	0·008	0·090	0·012
Siphunculus	0·167^{ns}	0·018	0·164^{ns}	0·029	0·190	0·018	0·150	0·026
Cauda	0·114^{ns}	0·014	0·116^{ns}	0·018	0·126	0·009	0·103	0·017
No. of specimens	257		429		28		88	
No. of samples	15		32		1		7	

ALATAE	$2n = 10$ Mean	s.d.	$2n = 8$ (homozygous) Mean	s.d.	$2n = 9$ Mean	s.d.
Body length	1·66^{ns}	0·27	1·65^{ns}	0·26	1·40	0·25
AS3	0·277*	0·052	0·269*	0·050	0·211	0·043
AS4	0·147^{ns}	0·031	0·146^{ns}	0·026	0·116	0·019
AS5	0·136*	0·025	0·132*	0·022	0·102	0·016
AS6 base	0·102^{ns}	0·012	0·102^{ns}	0·012	0·087	0·010
AS6 PT	0·237***	0·029	0·213***	0·029	0·186	0·026
URS	0·086***	0·005	0·084***	0·006	0·079	0·006
HT2	0·096**	0·008	0·098**	0·009	0·083	0·007
Siphunculus	0·136^{ns}	0·011	0·138^{ns}	0·015	0·108	0·014
Cauda	0·101***	0·011	0·106***	0·012	0·089	0·010
No. of specimens	323		277		43	
No. of samples	23		26		3	

Levels of significance only recorded for comparison of the eight- and ten-chromosome karyotypes. (* $P<0·05$; ** $P<0·01$; *** $P<0·001$; ^{ns} not significant.)
† Abbreviations as in Table II.

characters conformed, with relatively low variances, to the overall means for all samples of the karyotype.

None of the first five principal component axes separated the eight-chromosome and ten-chromosome samples. The least overlap was shown in plots involving the first three principal components. Specimens from the same sample usually had similar scores on at least two of the first three axes, and grouped together in plots involving them (Fig. 6*a* & *b*). Most of the samples suspected of genetic heterogeneity also formed groups at least as compact as those samples selected for their homogeneity, and there were only one or two instances of individuals with principal component scores markedly different from other members of the same group, i.e. possible 'contaminants'. Thus there was no basis for excluding any samples from the canonical variates analysis on grounds of heterogeneity, other than the one Idaho sample (no. 3527) that had definitely included both eight- and ten-chromosome individuals.

Rearing temperature had a considerable effect on morphology, and in particular all except one of the individual apterae of the ten-chromosome clone no. 2501 reared at 20°C had markedly different scores on axis 2 from those reared at other temperatures.

Canonical variates analysis.—Mean scores for the first five canonical variates (CV's) for each sample of the full data set were compared on the assumption that individuals collected at one place and time belonged to a single clone, and that the canonical variates analysis was therefore, in effect, maximizing the differences between genotypes.

In the first analyses, samples of all five karyotypes were included (e.g. Fig. 7). Subsequently, only the ten-chromosome samples and those homozygous for $2n = 8$ were

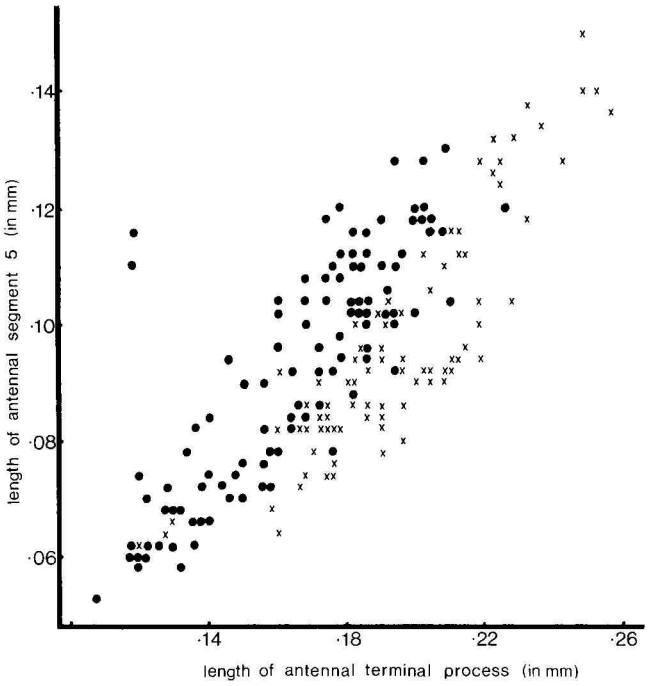

Fig. 2.—Plot of the lengths of the fifth antennal segment against the antennal terminal process for individual apterae of *Rhopalosiphum maidis* from samples karyotyped as $2n = 8$ (black circles) and $2n = 10$ (crosses).

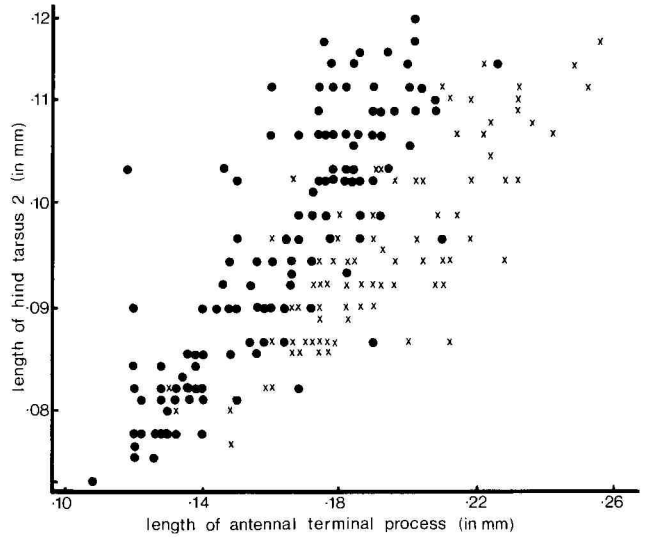

Fig. 3.—Plot of the lengths of the second segment of the hind tarsus against the antennal terminal process for individual apterae of *Rhopalosiphum maidis* from samples karyotyped as $2n = 8$ (black circles) and $2n = 10$ (crosses).

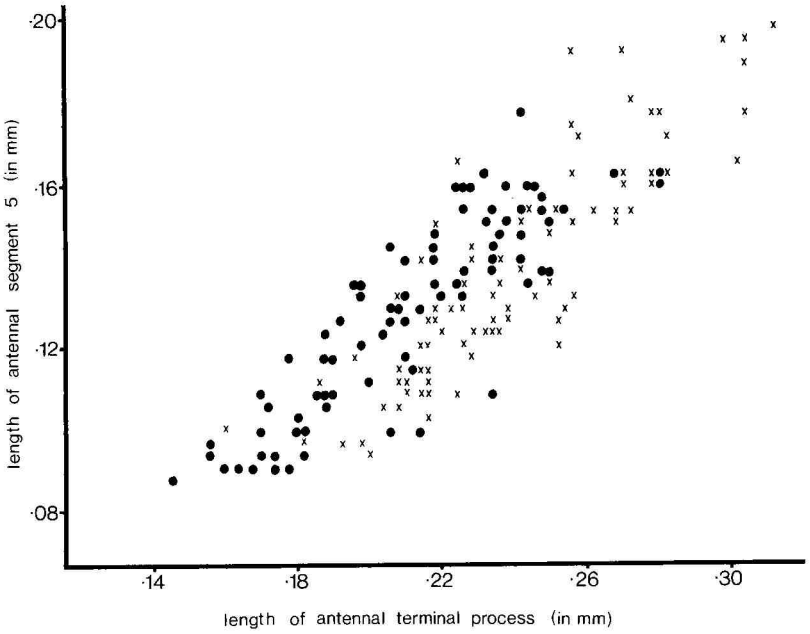

Fig. 4.—Plot of the lengths of the fifth antennal segment against the antennal terminal process for individual alatae of *Rhopalosiphum maidis* from samples karyotyped as $2n = 8$ (black circles) and $2n = 10$ (crosses).

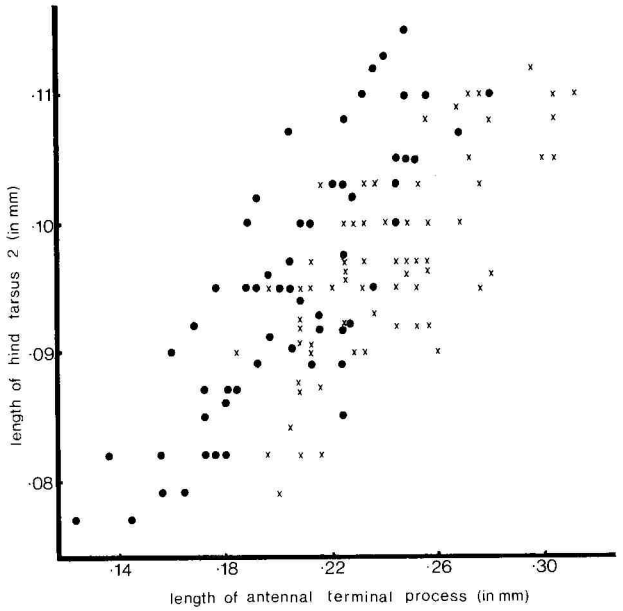

Fig. 5.—Plot of the lengths of the second segment of the hind tarsus against the antennal terminal process for individual alatae of *Rhopalosiphum maidis* from samples karyotyped as $2n = 8$ (black circles) and $2n = 10$ (crosses.)

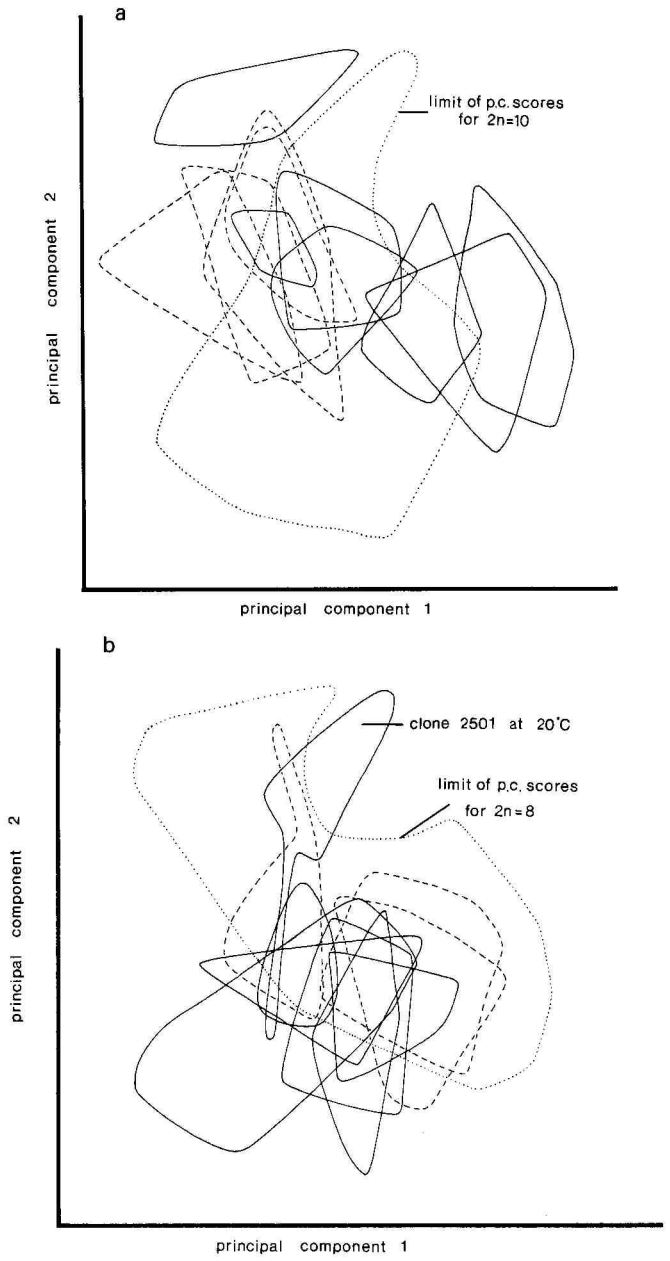

Fig. 6.—Plot of the first two principal components for samples of apterae of *Rhopalosiphum maidis*: (*a*) 11 samples karyotyped as $2n = 8$ and (*b*) ten samples karyotyped as $2n = 10$. In each plot, the limits of the principal component scores for individual apterae are indicated by solid lines for the samples known or believed to be genetically homogeneous, and by dashed lines for those suspected of heterogeneity. The dotted line in each case, indicates the limits of the principal component scores of the samples of the other karyotype.

included to concentrate on the separation of these two karyotypes (e.g. Fig. 8). Omitting the other three karyotypes did not, however, improve the separation of the eight- and ten-chromosome samples.

The first canonical variate was strongly size-dependent, and contributed very little to the separation of either karyotypes or groups. CV 2 provided the best, although not complete separation of ten-chromosome samples from other karyotypes. Variable 6, the antennal terminal process, made by far the greatest contribution to CV 2, followed by variables 4 (fifth antennal segment) and 8 (hind tarsus second segment).

Samples of the same ten-chromosome clone reared at different temperatures differed greatly in their scores on both CV 1 and CV 2, and it was clear that the scatter of the values of ten-chromosome samples could be explained solely in terms of the effects of environmental differences on a single genotype.

Of the seven 9-chromosome samples included in the analysis of apterae, six had very similar scores on CV 2 (e.g. Fig. 7). Three of these were from Iran and three from the USA, the odd one out being from Tasmania.

The scores on CV's 3, 4 and 5 were also examined, but these all showed strong environmental effects and failed to provide any meaningful grouping of samples.

Of the four samples of Painter & Pathak's Kansas biotypes, KS-1 and KS-2 (which both originated from sorghum according to Painter & Pathak (1962)) grouped with the ten-chromosome samples, and KS-4 (which originated from barley) grouped with the eight-

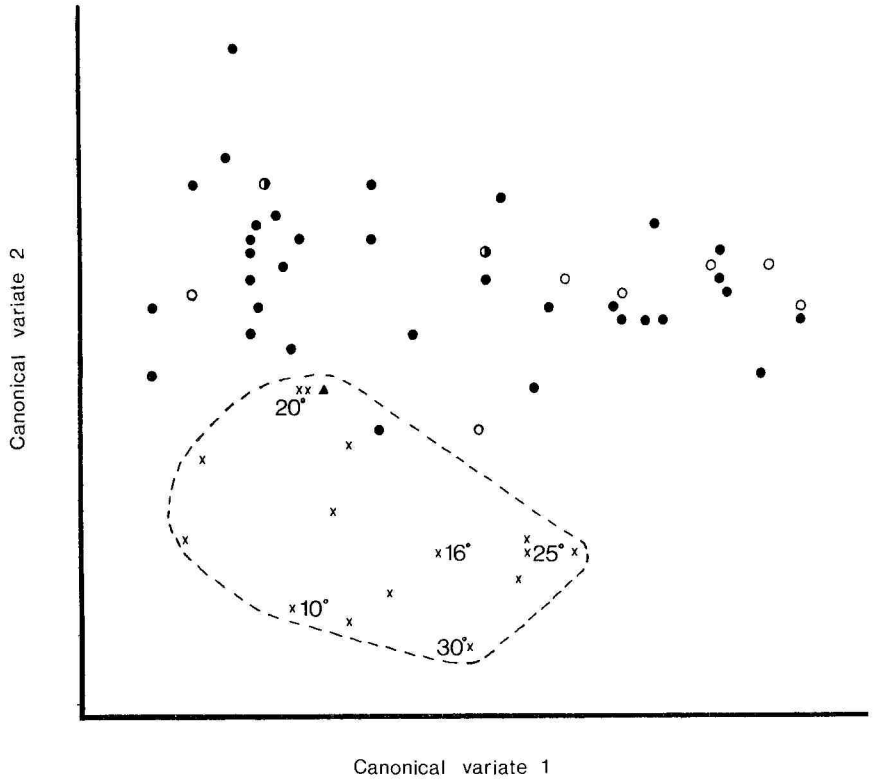

Fig. 7.—Plot of the mean scores on the first two canonical variates for samples of apterae of *Rhopalosiphum maidis* karyotyped as $2n = 10$ (crosses), $2n = 8$ homozygous (black circles), $2n = 9$ (open circles), $2n = 8$ heterozygous (half-black circles) and $2n = 11$ (black triangles).

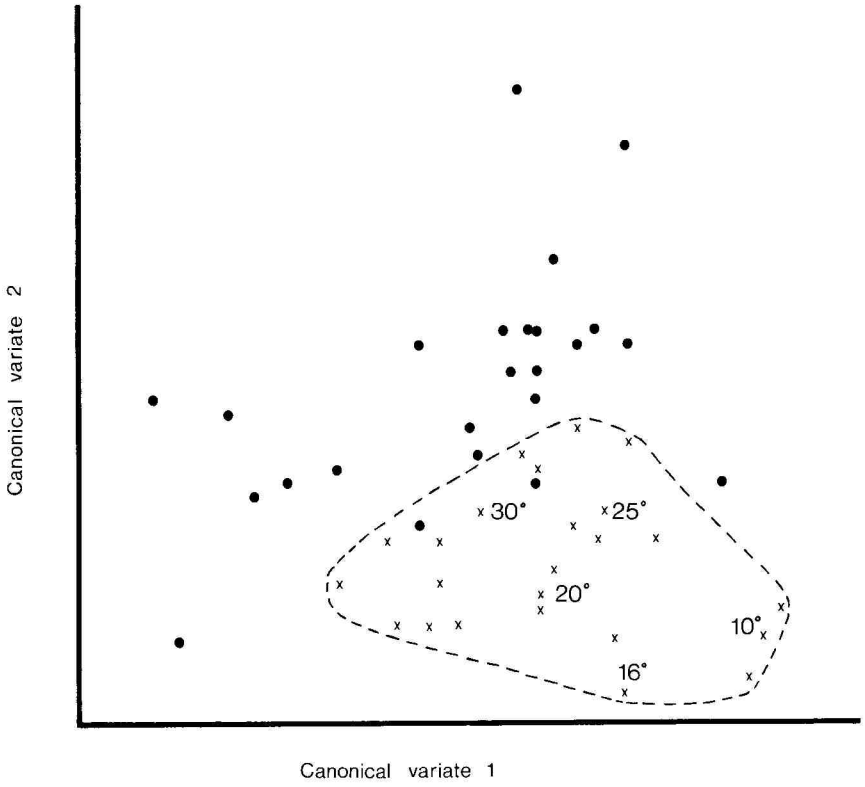

Fig. 8.—Plot of the mean scores on the first two canonical variates for samples of alatae of *Rhopalosiphum maidis* karyotyped as $2n = 10$ (crosses) and $2n = 8$ homozygous (black circles).

chromosome samples. This is the reverse of what was expected. The sample of KS-3 (originally from wheat) occupied an intermediate position.

Discussion

It is possible that better morphometric separation could have been achieved between karyotypes if all samples used in the canonical variates analysis had been of known clonal composition. However, this is by no means certain. It appears that the ten-chromosome samples of *R. maidis* can be regarded as a single clone, characterized by its karyotype and host-plant affinities, but not completely separable by morphology alone from all other clones of *R. maidis*. The failure to obtain a complete morphological separation could be for two reasons: (1) the apparently strong interaction between environmental and genetic components of morphological variation in *R. maidis*, so that no canonical variate is completely independent of environmental conditions such as temperature, and (2) the permanent apomixis of the species as a whole on a worldwide basis, giving rise to a situation where the ten-chromosome form is just one widely distributed clone among many. This might seem to be at variance with the fact that the overall means of certain characters differ significantly between eight- and ten-chromosome samples (Table V). The explanation may be that there are one or two common and widespread clones with $2n = 8$ which are morphologically distinguishable from the ten-chromosome form, but other less common clones are also present which have a greater morphological resemblance to the ten-chromosome form and thus blur the distinction.

On the basis of the evidence here presented, one may conclude that a genotypically distinct form of *R. maidis* occurs on barley in the northern hemisphere, and that this form does not colonize *Sorghum* spp. or maize. Furthermore, the populations that occur on *Sorghum* and maize do not normally colonize barley. This conclusion has certain obvious economic implications. Other Gramineae may be colonized by *R. maidis* populations of various karyotypes, although nine- and ten-chromosome forms seem to be more common than those with eight chromosomes on the eupanicoid grasses of the genera *Setaria*, *Echinochloa*, *Digitaria* and *Panicum*. In Idaho, aphids collected in roadside ditches on *E. crus-galli*, *S. pumila* and *P. capillare* all had ten chromosomes, whereas those from maize in neighbouring fields were all $2n = 8$ (S. E. Halbert, pers. comm.).

Work is in progress to define the best discriminants for morphological recognition of apterae and alatae of the ten-chromosome form. Further work will be necessary to show whether samples of eight-chromosome forms of *R. maidis* fit into a finite number of groupings, and to establish whether each of the other karyotypes should be regarded as one clone or many. Such work requires the rearing of more clones in different environments. Interpretation of morphometric analysis would also be greatly assisted if it were complemented by electrophoretic studies on the same clonal material.

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