

The electromagnetic field waveform of the pulse signal and its first time-derivative (below) measured using a calibrated search coil. The magnetic fields with various intensities used in the present work were generated by a 25-μs pulse, repeating at 100 Hz.

Physical agents, such as UV or ionizing radiations, increase the SCE frequency^{11-13, 15, 16} and drugs, such as bleomycin or adriamycin, which are known to intercalate into or break the DNA molecules, have also been shown to increase the SCE frequency^{14, 20, 21}. Contrary to these agents, which can modify the DNA molecules themselves, magnetic fields with an intensity in the range from 0.18 to 2.5 mT do not seem to damage DNA in cells which are entering the M phase of the cell cycle, thereby leading to an increased frequency of SCE.

The possible mechanisms involved in the modification of a variety of biological processes by magnetic fields are still largely unexplained at present. The present results show that magnetic fields with 0.18–2.5 mT seem to lack the ability to induce SCEs in cultured Chinese hamster cells. The intensities used here amount to 3.6–50-fold of the geomagnetic field; however, the magnetic fields produced by modern generators, such as those used for clinical diagnoses, have magnetic intensities far larger than those used here. Further investigations with the use of other cell types

as well as other experimental conditions would be required to assess possible risk effects of magnetic fields.

Acknowledgments. We thank M. Ohara (Kyushu Univ.) for critically reading the manuscript. This work was supported by KAKEN Pharmaceutical Co., Ltd., Tokyo, Japan, and in part by a Grant-in-Aid from the Ministry of Education, Science and Culture of Japan and from the Foundation for Life Science Promotion, Tokyo, Japan, to I.K.

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0014-4754/87/0331-02\$1.50 + 0.20/0
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Extra-nuclear inheritance in a sexually produced aphid: the ability to overcome host plant resistance by biotype hybrids of the greenbug, *Schizaphis graminum*

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Summary. Greenbugs of biotype E that grow and reproduce well on a biotype C-resistant sorghum (IS 809) were crossed with biotype C greenbugs. The resulting hybrids were tested on IS 809 to study how the ability to overcome the cultivar's resistance is inherited. Only those hybrids stemming from biotype E mothers were able to overcome the resistance of IS 809 plants, indicating that this trait is inherited by the sexually-produced fundatrices in an extra-nuclear manner from the mother. A plausible explanation for this phenomenon is presented.

Key words. Extra-nuclear inheritance; aphids; greenbugs; *Schizaphis graminum*; biotypes; hybrids; fundatrix; plant resistance; symbiotes.

The rapid evolution of aphid biotypes able to overcome resistance bred into graminaceous plants is well documented for the greenbug, *Schizaphis graminum* (Rondani)^{1, 2}, the most destructive insect attacking small grains in the Great Plains region of the USA³. Most of the seasonal generations of the aphid are produced by asexual parthenogenetic reproduction. Each aphid

thereby gives rise to genetically identical progeny and it is difficult therefore to elucidate the mechanism of inheritance of biotype traits. Under fall conditions, however, the aphid can reproduce sexually, and, from fertilized overwintering eggs, spring generations are produced by fundatrices which differ genetically from each other. This paper reports on the inher-

itance of the ability of a biotype (E) of *S. graminum* to overcome the resistance of a variety of *Sorghum bicolor* to biotype C of the aphid, when sexuals of the 2 biotypes are crossed.

Materials and methods. Two holocyclic clones of *S. graminum* were used to make the crosses: the C biotype from Stillwater, Oklahoma, and the E biotype from Lincoln, Nebraska. The aphids were maintained in culture on seedlings of a non-resistant barley (*Hordeum vulgare*) variety CM 72, at 18–20°C in a 16 h light:8 h dark regime (referred to as LD 16:8).

The males and oviparae used for making the various crosses of the 2 biotypes were produced on barley seedlings in a LD 9:15 regime⁴. The techniques for mating the sexuals, and for collecting, surface sterilizing and incubating their eggs, have recently been described⁵. Few, if any, of the fundatrices survived and developed on the CM 72 barley. Therefore, the suitability of a number of other graminaceous plants, known to be hosts of *S. graminum*, were evaluated for rearing the fundatrices. These plants included varieties of Kentucky blue grass, *Poa pratensis*, on which eggs of *S. graminum* have been recorded in nature⁶. Only on the common Kentucky blue grass did some of the fundatrices survive⁷. Those fundatrices that reached adulthood were transferred to and maintained individually on CM 72 barley seedlings where they gave rise to the various clones that were maintained at 18–20°C and LD 16:8.

Fourteen experimental clones were established, comprising 5 clones of EE, 3 clones of EC, 3 clones of CE, and 3 clones of CC. The first letter in each cross designates the maternal biotype and

Table 1. Mean number of offspring per adult apterous virginopara of *S. graminum* for each clone after one generation on C-resistant sorghum, IS 809

Clone	Parental E	Crosses				Parental C
		EE	EC	CE	CC	
1	44.3	44.0	38.6	19.8	17.9	20.9
2		41.1	34.3	17.2	24.6	
3		39.9	38.3	22.3	17.6	
4		39.8				
5		42.3				
\bar{x}^*	44.3	41.5	36.8	19.8	20.0	20.9
SD	± 4.5	± 8.0	± 6.9	± 5.1	± 6.5	± 2.5
(n)	(7)	(35)	(21)	(21)	(24)	(7)

*Values based on data for (n) individuals from each cross.

Table 2. Mean weights (μg) of adult apterous virginoparae for each clone of *S. graminum* after one generation on C-resistant sorghum, IS 809

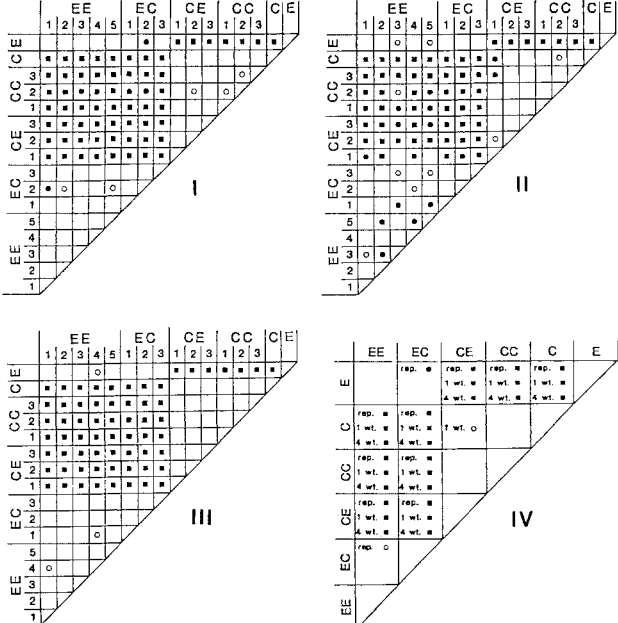
Clone	Parental E	Crosses				Parental C
		EE	EC	CE	CC	
1	299.7	293.1	322.4	212.4	179.4	140.0
2		312.8	276.1	159.6	187.9	
3		244.4	299.8	178.9	151.8	
4		321.1				
5		250.9				
\bar{x}^*	299.7	284.5	299.4	183.6	173.0	140.0
SD	± 48.5	± 53.9	± 44.3	± 54.1	± 41.5	± 24.2
(n)	(7)	(40)	(24)	(24)	(24)	(7)

*Values based on data for (n) individuals from each cross.

Table 3. Mean weights (μg) of adult apterous virginoparae for each clone of *S. graminum* after 5 generations on C-resistant sorghum, IS 809

Clone	Parental E	Crosses				Parental C
		EE	EC	CE	CC	
1	185.7	186.6	113.8	98.6	106.9	
2		200.0	192.1	104.0	94.8	
3		192.7	200.8	114.7	100.1	
4		206.4				
5		186.9				
\bar{x}^*	185.7	194.4	193.4	110.3	98.1	106.9
SD	± 22.6	± 24.5	± 15.1	± 17.3	± 22.1	± 15.8
(n)	(7)	(46)	(28)	(18)	(19)	(8)

*Values based on data for (n) individuals from each cross.



Figures I–IV. The significance levels (■ $p < 0.001$, ● $p < 0.01$, ○ $p < 0.05$) for pairwise statistical comparisons of the data: I, for the mean number of nymphs produced by clones by biotype C and E and of their sexually produced lineages CC, CE, EC and EE (where the first letter denotes the maternal biotype) when raised on a C-resistant variety of sorghum IS 809; and II and III, for the adult weights attained by these clones after 1 or 5 generations, respectively, on IS 809. IV summarizes the differences between the clones for these attributes.

the second letter the paternal biotype. Clones of the original 2 parental biotypes, C and E, served as controls.

After 5 successive generations on the barley, the relative performance of the clones was tested on the biotype C-resistant sorghum IS 809. Specifically, 2–3-day-old adults of each clone were confined for a few hours on IS 809 seedlings (10 days after sowing) and when their young (designated G_1) became adult (all were apterous virginoparae), 8 aphids from each clone were weighed individually on a torsion balance and placed singly on fresh seedlings of IS 809. Every 2–4 days throughout their adult lives, the aphids were transferred to new seedlings of IS 809 and serial records kept of the number of their G_2 offspring.

To determine whether the relative responses of the 16 clones are maintained for several successive generations on the IS 809 plants, G_2 nymphs from each of these clones were used to initiate 3 additional generations on IS 809. Apterous adult virginoparae of the fifth generation (G_5) were then weighed individually. The results were subjected to a nested analysis of variance and multiple range test.

Results and discussion. Table 1 records the mean number of nymphs produced during the life span of the G_1 aphids of the parental and hybrid clones on the sorghum IS 809. The overall results show that twice as many nymphs were produced by the parental E clone and by the sexually produced clones with E mothers than by the C clone and the sexually produced clones with C mothers. Pairwise statistical comparisons of the data (fig. I) confirm these major differences; they also reveal some differences between maternal E clones, due largely to the relatively poor performance of the EC_2 hybrid.

The mean weights of the G_1 aphids on attaining adulthood on the IS 809 sorghum are presented in table 2. The overall results show that aphids of the parental E clone and hybrids with E mothers attain adult weights that are 50–100% higher than aphids of the C clone and hybrids with C mothers. Pairwise statistical comparisons (fig. II) highlight these differences but reveal some inconsistencies, largely due to the low weights at-

tained by 2 of the 5 EE clones. The EE₃ and EE₅ clones in question nevertheless produced considerably more nymphs than any of the maternal C aphids of similar weight (tables 1 and 2). The mean weights of young adult aphids of each clone after a further 4 generations on the IS 809 sorghum are given in table 3. The relative performance of these G₅ clones (fig. III) is the same as that of the G₁ aphids (fig. II). However, less variability occurred between clones of the same crosses, and the performance of all the clones was some 50% poorer than that of the G₁ aphids. Because the mothers of the latter had developed on susceptible barley (on which they grew twice as big and produced 70–80 nymphs) it is possible that nutritional factors passed transovarially to the G₁ aphids enabled them to grow substantially better than the later generations on the IS 809 sorghum.

As summarized in figure IV, the results indicate that it is the maternal biotype which determines if an individual *S. graminum* can overcome plant resistance. This pattern of inheritance cannot be explained in Mendelian terms. Possible explanations for the phenomenon include extra-nuclear inheritance and parthenogenetic development of the eggs. While parthenogenesis is the mode of reproduction by viviparous aphids, it is unlikely that it takes place in the winter eggs of aphids, because the few eggs that virgin oviparae may deposit do not turn black (as do the majority of the eggs deposited by mated oviparae) and they shrivel when incubated. On the other hand, cytoplasmic transmission of symbiotic microorganisms from oviparae to their eggs is well documented⁸, and extra-nuclear inheritance has been shown to affect the fitness of insect populations in various ways⁹.

The symbiotes of aphids appear to play important roles in the nutrition of their hosts by providing them with some essential nutrients^{10–12}. That the symbiotes may also provide aphids with certain enzymes that are able to hydrolyze plant matrix polysaccharides has been inferred for *S. graminum*. These enzymes have

been surmized to facilitate inter-cellular penetration of plant tissues by the aphid's stylets, with an increase in enzyme activity in biotype E being correlated with the ability to overcome this host plant barrier in biotype C-resistant sorghum plants^{13, 14}. The breakdown products of these hydrolyses may also make the plant more acceptable to the aphids¹⁵. Such attributes have been invoked to explain the ability of *S. graminum* to overcome resistance in sorghum, and may have been acquired as a result of the rapid generation turn-over of its symbiotic microorganisms¹⁶. The maternally-related performance of the hybrids may best be explained in terms of the extra-nuclear inheritance by the aphids of symbiotes from their mothers.

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0014-4754/87/0332-03\$1.50 + 0.20/0

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Chronic mercury vapor poisoning of aphids

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Summary. Exposure of green peach aphids, *Myzus persicae* (Sulz.), to an atmosphere containing mercury vapor resulted in a curtailment of embryogenesis and larviposition by adults, and in the development by larvae and adults of a cuticular darkening of their legs, head capsule, antennae, cornicles and cauda. Mortality of affected larvae resulted from molting difficulties, particularly by last-instar alatiform female and male larvae. Greenbugs, *Schizaphis graminum* (Rond.), and pea aphids, *Acyrtosiphon pisum* (Harr.), responded to mercury vapor exposure in similar ways.

Key words. Aphids; green peach aphids; *Myzus persicae*; greenbug; *Schizaphis graminum*; pea aphid; *Acyrtosiphon pisum*; mercury vapor; contamination; pigmentation; reproduction.

In a clonal culture of the green peach aphid (a biotype of *Myzus persicae* (Sulz.) from Yakima, Washington State) maintained in one of our temperature- and light-controlled cabinets, we detected several aphids of apparently another species. These aphids were of similar shape to the *M. persicae* but their bodies were conspicuously yellowish, and their antennae, legs, cornicles and cauda were dark grey or black, and some had a dusky head capsule. The presence of these aphids was at first ascribed to contamination by stray aphids of the greenhouse-grown radish seedlings on which the culture was maintained. However, after the establishment of a new clonal culture of the *M. persicae*, some of the unusual aphids were again found together with normal aphids on each of the radish seedlings placed in the same cabinet. This was the case despite close scrutiny of the plants for possible strays, the plants' individual confinement within screen-topped plastic cages, and the absence of any other aphid/plant cultures in this cabinet.

Careful inspection of the affected cabinet revealed a few small beads of mercury in crevices on its floor. These stemmed from a

broken thermometer that had otherwise been removed from the cabinet a week before the first observation of the unusual aphids. Since the cabinet, a modified 280-l refrigerator, was almost airtight, it appeared possible that a mercury vapor build-up within it could have been responsible for the observed changes in the aphids.

The present paper describes some of the experiments which tested this possibility and evaluated the effects of exposing various morphs of *M. persicae* and 2 other aphid species to mercury vapor at levels that could arise under accidental circumstances such as described above.

Methods and results. When *M. persicae* larvae were allowed to develop from birth on radish seedlings confined in a 9-l desiccator jar containing a single bead (0.2 g) of mercury, the majority of the larvae developed the unusual characters. Many of the aphids died before reaching adulthood and most of those that became adult were sterile. The radish seedlings were also severely affected by this treatment. There was an early yellowing of their cotyledons, a curling of the cotyledons and of the primary