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Effect of European wheat striate mosaic, acquired transovarially, on the biology of its planthopper vector *Javesella pellucida*

By E.-D. AMMAR*

Nottingham University School of Agriculture, Sutton Bonington, Notts

(Accepted 14 August 1974)

SUMMARY

The proportion of infective nymphs of *Javesella pellucida* in the progenies of female vectors of European wheat striate mosaic (EWSM) disease ranged from 85 to 96 %; 71 % of these nymphs infected plants within one week of hatching. Inbreeding for one or two generations significantly decreased the viability of *J. pellucida* eggs, but EWSM had no effect on the viability of eggs laid by inbred or outbred vector lines. However, EWSM acquired transovarially usually increased the mortality of *J. pellucida* nymphs by 13 to 17 %, although mortality was as high as 30 % in some vector lines. EWSM, acquired transovarially for two generations, decreased the longevity of adult males and females of *J. pellucida* by 14 %. Inbreeding for two generations resulted in 40 % increase in the mortality of nymphs and more than 50 % reduction in the longevity of adults.

INTRODUCTION

European wheat striate mosaic (EWSM) disease is transmitted transovarially to a large proportion of the progeny of infective females of *Javesella pellucida* (Fab.) (Slykhuys & Watson, 1958). Kisimoto & Watson (1965) failed to confirm previous reports (Watson & Sinha, 1959; Sinha, 1960) that EWSM caused pathological effects in the eggs of this vector, but found that gross abnormalities in these eggs resulted from inbreeding. Sinha (1968), however, suggested that *J. pellucida* eggs might be damaged more at a later stage of embryonic development by EWSM than they were by inbreeding. Using outbred lines of *J. pellucida*, Ammar (1975) found no pathological effects of EWSM acquired by first and second instar nymphs from diseased plants, on the nymphal and adult stages or on the hatchability of eggs laid by infective females.

The present investigation was undertaken to study the effects of inbreeding and of EWSM acquired transovarially on the survival of the embryonic, nymphal and adult stages of *J. pellucida*. The occurrence of embryonic abnormalities in inbred eggs laid by infective and non-infective females of this vector was also investigated.

MATERIALS AND METHODS

The sources of planthoppers and EWSM, the methods of culturing and testing them and the lineage-designation system used for the vector are as described previously

* Present address: Plant Protection Department, Faculty of Agriculture, Cairo University, Egypt.

(Ammar, 1975). Experiments were usually done in a temperature-controlled cabinet at 19–22 °C, but one was done in a glasshouse with temperatures of 15–20 °C during the day and a minimum of 10 °C at night. Photoperiod in all experiments was 18 h/day. Watson & Sinha (1959) studied transovarial transmission of EWSM in *J. pellucida* by removing the eggs of the vector from the plant tissues and incubating them on moistened filter paper. This precluded hatched nymphs from feeding on possibly infected plants; under these conditions hatching was poor, and results suggested that leaving the eggs in the host plant and isolating the nymphs shortly after hatching provided a better test for transovarial transmission than did the isolation of eggs before hatching. Their results were confirmed in the present work; nymphs were therefore removed within 24 h of hatching and tested for infectivity on healthy wheat seedlings. Test seedlings were kept under observation in the glasshouse for 5 to 6 wk after removal of the hoppers.

RESULTS

Effect of EWSM on inbred eggs of Javesella pellucida

Eggs were obtained in two successive weeks from 2 to 3-wk old, brother-to-sister mated, pairs of *J. pellucida*. Twenty-three pairs were non-infective and had never fed on diseased plants, nineteen pairs had fed on diseased plants (exposed) for 7 days in their early nymphal stage but did not become infective, and twenty-three pairs were similarly exposed but the females and some of the males became infective. Eggs were incubated in the host wheat seedlings until hatching; 1 wk after hatching had stopped, seedlings were dissected and examined for unhatched eggs and empty egg shells. The unhatched (non-viable) eggs were grouped into the following categories:

Undeveloped: eggs that showed no externally visible sign of embryonic development. *Pre-blastokinetic*: eggs that had the rounded yellow mycetome near the anterior pole and had no visible eye spots.

Mid-blastokinetic: eggs with the yellow mycetome midway between the anterior and posterior poles, indicating that blastokinesis had started in these eggs but was not successfully completed.

Post-blastokinetic: eggs with the yellow mycetome at the posterior pole, and two red eye spots near the anterior pole.

Partially hatched: eggs in which hatching was incomplete with the embryo half-way through the egg cap.

Abnormal embryos: (a) *dwarf*: embryos shorter than normal, occupying only about two-thirds of the space inside the egg shell.

(b) *reversed*: embryos which had failed to undergo blastokinesis, and were in a reversed position, with the red eye spots near the posterior pole of the egg.

(c) *other abnormalities*: eggs showing abnormalities other than those described above; e.g. distorted or mis-located mycetomes and eye spots, or disturbed yolk system. Numbers of eggs obtained in two weeks from the twenty-three unexposed, nineteen non-infective exposed, and twenty-three infective females were 2722 (mean 118.3), 2041 (mean 107.4) and 2680 (mean 116.5) respectively; 33–47% of these eggs were non-viable (Table 1). The highest proportion (67–70%) of non-viable eggs occurred in the post-blastokinetic category. Analysis of variance, after angular transformation

of the data, showed that only the differences between various categories of non-viable eggs were significant, but those between unexposed, non-infective exposed and infective groups were not.

These results show that EWSM acquired orally by the mothers in their early nymphal stage did not increase the proportion of non-viable eggs laid, or modify the stages at which embryonic abnormalities occurred in inbred eggs of the vector.

Table 1. *Percentage of non-viable eggs laid by brother-to-sister mated females of *Javesella pellucida*, either exposed* or unexposed to EWSM-diseased plants*

Category of non-viable eggs	Mothers		
	Unexposed Non-infective	Exposed	
		Non-infective	Infective
Undeveloped	5.5	4.5	5.0
Pre-blastokinetic	2.2	1.1	1.2
Mid-blastokinetic	0.5	0.0	0.0
Post-blastokinetic	33.4	28.1	22.0
Partially hatched	0.5	0.7	1.5
Abnormal			
Dwarf	0.2	0.1	0.1
Reversed	4.3	1.8	2.5
Others	0.3	0.1	0.8
Total non-viable eggs	46.9	36.4	33.1

S.E. (arc sine), 1.93. Treatment means (arc sine \pm 0.68): unexposed, 10.4; exposed non-infective, 8.4; exposed infective, 9.1.

* Exposed hoppers were fed on diseased plants for 7 days in the early nymphal stage; 2044-2722 eggs were examined from each group of mothers; percentage values are detransformed from arc sine.

Table 2. *Infectivity* of *Javesella pellucida* nymphs obtained from inbred and outbred pairs in which the females only were infective with EWSM*

Inbred nymphs				Outbred nymphs			
Line	No. tested	Infective		Line	No. tested	Infective	
		No.	%			No.	%
KK1	33	30	90.9	GJ	70	66	94.3
KK2	17	16	94.1	JH1	57	50	87.7
GG	13	11	84.6	JH2	73	70	95.9
Total	63	57	90.5	Total	200	186	93.0

* Nymphs were tested singly for infectivity for 3 weeks after hatching.

*Proportion of *Javesella pellucida* nymphs inheriting EWSM from infective mothers*

Eggs were obtained from six infective *J. pellucida* females, that had acquired EWSM by feeding on diseased plants in their early nymphal stage. Three of these females were mated with their non-infective brothers (inbred) and three were mated with non-infective males from other lines (outbred). Newly hatched nymphs were caged singly on healthy wheat seedlings to test their infectivity. Tests were conducted over three weeks, by the end of which all the surviving nymphs had become adults.

Of the sixty-three nymphs from the inbred group, 91% were infective; in the outbred group, 93% of the 200 nymphs were infective (Table 2). The proportion of infective hoppers did not differ significantly between inbred and outbred groups ($\chi^2 = 0.43$) or between males and females and unsexed individuals of the vector (Table 3, $\chi^2 = 3.37$, D.F. = 2).

Of all the hoppers tested, 71% proved infective in the first week after hatching (Table 3), 18% more became infective in the following week and a further 3% proved infective in the third week. No interaction was found between the sex of the individual and the time of its becoming infective after hatching.

Table 3. Infectivity of *Javesella pellucida* nymphs, progenies of infective females, classified according to sex and time (in weeks) after hatching when infectivity was first demonstrated

Sex*	No. nymphs tested	No. nymphs infective				% nymphs infective			
		Wk 1	Wk 2	Wk 3	Total	Wk 1	Wk 2	Wk 3	Total
Male	112	77	23	4	104	68.8	20.5	3.6	92.9
Female	99	71	19	4	94	71.7	19.2	4.0	94.9
Unsexed	52	39	6	0	45	75.0	11.5	0.0	86.5
Total	263	187	48	8	243	71.1	18.3	3.0	92.4

* Sex was determined when nymphs attained adulthood; unsexed individuals died earlier.

Table 4. Effects of inbreeding and inherited EWSM on the percentage survival of *Javesella pellucida* throughout the nymphal stage

Treatment and line	Initial no. of nymphs	Days after hatching (± 3.5 days)					Survival to adult
		5	10	15	20	25	
Non-infective outbred							
CD	175	92.0	92.0	89.7	89.1	84.6	84.0
DC	190	87.4	81.1	77.9	77.4	74.7	74.2
Total	365	89.6	86.3	83.6	83.0	79.5	78.9
Non-infective inbred							
CC	138	81.2	74.6	68.8	67.4	65.2	64.5
DD	150	81.3	70.0	65.3	60.7	58.0	56.7
Total	288	81.3	72.2	67.0	63.9	61.5	60.4
Congenitally infective							
CC inbred	81	74.1	61.7	53.1	48.1	46.9	43.2
DD	60	70.0	65.0	63.3	60.0	60.0	60.0
Total	141	72.3	63.1	57.4	53.2	52.5	50.4

Effects of EWSM and inbreeding on survival of Javesella pellucida nymphs to adulthood

Three categories of nymphs were compared: (a) non-infective outbred, obtained from six non-infective pairs, three of line CD and three of line DC; (b) non-infective inbred, obtained from six brother-to-sister mated non-infective pairs, three of line CC and three of line DD; (c) congenitally infective inbred, obtained from five females that proved infective as a result of feeding on diseased plants and mated to their non-infective brothers (three pairs of line CC and two of line DD). Newly hatched nymphs from eggs laid within one week by each of the above pairs were caged on one pot of

healthy wheat seedlings. Nymphs were counted at 5-day intervals and transferred until adulthood to healthy seedlings every 10 days.

None of the plants on which the progenies of non-infective pairs had fed became infected, whereas those on which the progenies of infective females had fed showed clear symptoms of EWSM.

The proportion of nymphs surviving to adulthood was 76% in the non-infective outbred, 58% in the non-infective inbred and 40% in the congenitally infective inbred groups (Table 4). The difference in survival, due to inbreeding, between the first two groups is highly significant ($\chi^2 = 24.6$, $P < 0.001$), as is the difference between the two inbred groups, presumably due to transovarially transmitted EWSM ($\chi^2 = 11.2$, $P < 0.001$).

The greater mortality in congenitally infective hoppers, compared to that of non-infective (inbred) ones, was much higher in line CC (27%) than in line DD (5.7%). This might have been due to differences in rates of transovarial transmission between the two lines or to differences in their susceptibility to the deleterious effects of transovarially transmitted EWSM. In the previous generation, line C (parents of CC) was much more efficient in acquiring EWSM from diseased plants (89%) than was line D (29%) (Ammar, 1975). However, in the previous experiment (Table 2), over 84% of *J. pellucida* nymphs acquired EWSM transovarially irrespective of their lineage. Therefore, it is more likely that nymphs of line CC differed from those of line DD in their susceptibility to the effects of EWSM rather than differing in their rates of transovarial transmission.

As the figures in Table 4 indicate, the difference in the proportion of surviving nymphs between outbred and inbred (non-infective) groups was apparent on the fifth day after hatching ($\chi^2 = 9.3$, $P < 0.01$), as was the difference on this day between non-infective (inbred) and congenitally infective groups ($\chi^2 = 4.4$, $P < 0.05$).

Effects of EWSM and inbreeding on survival and duration of the embryonic, nymphal and adult stages of Javesella pellucida

Three groups of hoppers were compared: (a) non-infective inbred, obtained from five non-infective females (line GG) that had been mated to their non-infective brothers for two successive generations; (b) non-infective outbred, obtained from three cross-mated non-infective pairs (lines KI and GJ); (c) congenitally infective outbred, obtained from four cross-mated pairs that had acquired EWSM by inheritance from infective mothers (lines JH and GJ). Thus in the latter group, EWSM had passed transovarially for two successive generations.

Nymphs hatching from eggs laid within one week by each of the above pairs were collected daily and caged on healthy wheat seedlings transplanted in specimen tubes (1 x 6 in; 2.5 x 15 cm). Maximum rearing density was twenty nymphs/seedling/tube in the first week after hatching, five and two nymphs/seedling/tube in the following two weeks respectively. Nymphs were counted every other day and transferred weekly to healthy seedlings; all seedlings were kept in the glasshouse for observation.

The adults emerging from the above nymphs were caged in groups on healthy wheat seedlings (maximum of twenty pairs/ten plants/pot). They were counted and transferred to healthy seedlings weekly until all were dead.

Viability and incubation period of eggs. The number of eggs produced in a 7-day period by inbred females was significantly lower ($P < 0.01$) than that of eggs produced by outbred ones (Table 5). Percentage of viable eggs also was lower in inbred eggs than in outbred ones ($P < 0.001$). The mean incubation period of the viable eggs laid by inbred females (11.5 days) was significantly shorter ($P < 0.001$) than that of the viable eggs laid by outbred ones, whether these were non-infective (12.1 days) or congenitally infective (12.3 days).

Table 5. *Survival and duration of the embryonic, nymphal and adult stages of non-infective and congenitally infective Javesella pellucida*

Attribute	Inbred				Outbred				Congenitally infective			
	Mean	S.E.	No.†		Mean	S.E.	No.†		Mean	S.E.	No.†	
Eggs												
No./female (in 7 days)*	40.2	4.9	5		74.7	4.9	3		64.0	4.9	4	
Viable eggs (%)*	40.8	—	201		85.7	—	224		86.3	—	256	
Incubation period (days)*	11.54	0.13	87		12.08	0.08	217		12.25	0.08	240	
Nymphs												
Survival to adult (%)**	54.4	—	92		94.0	—	167		80.9	—	236	
Nymphal duration (days)*	22.82	0.38	22		20.56	0.21	72		20.10	0.20	82	
Adults												
Female	25.39	0.43	28		21.66	0.25	83		21.34	0.22	109	
Sex ratio (% female)	56.0	—	50		53.8	—	156		57.1	—	191	
Longevity (days)**	10.93	1.30	22		21.12	1.45	69		18.20	1.07	82	
Male	13.37	2.43	26		41.94	1.96	85		35.62	1.58	111	
Female												

† No. of hoppers from which the information was obtained.
 * Indicates that the inbred group differs significantly from the two outbred ones but these do not differ significantly.
 ** Indicates that each of the three groups compared differs significantly from the rest.

However, there were no significant differences in the above attributes between the two outbred groups — non-infective and congenitally infective. Thus, EWSM transmitted transovarially did not affect the hatchability or the incubation period of outbred eggs of the vector.

Infectivity of nymphs produced by congenitally infective females. Nymphs of the congenitally infective (outbred) group were tested for infectivity in the first week after hatching on forty plants (1 to 20 nymphs/plant), in the second week on forty-nine plants (1 to 5 nymphs/plant) and in the third week on seventy-eight plants (1 to 2 nymphs/plant). Percentage of test plants that showed symptoms of EWSM was 93, 94 and 94 % in first, second and third weeks respectively. None of the plants fed upon by hoppers of the two non-infective groups (inbred and outbred) showed any disease symptoms.

Survival and duration of the nymphal stage. The proportion of nymphs surviving to adulthood (Table 5) was significantly lower in inbred hoppers than in outbred ones ($P < 0.001$); it was also lower in congenitally infective hoppers compared to non-

infective (outbred) ones ($\chi^2 = 12.7$, $P < 0.001$). The sex ratio did not differ significantly between hoppers of the three groups ($\chi^2 = 0.002-0.5$), with the percentage of females ranging between 54 and 57%. Thus, it seems that both inbreeding and transovarially transmitted EWSM independently caused early death of a proportion of *J. pellucida* nymphs, regardless of their future sex.

Within-treatment χ^2 analysis revealed that the three non-infective outbred progenies did not differ significantly in the proportion of nymphs surviving to adulthood (Table 6, $\chi^2 = 1.8$), but the four congenitally infective (outbred) progenies differed significantly in this respect ($\chi^2 = 32.8$, $P < 0.001$). In two of the latter progenies, survival to adulthood was over 95%, whereas in the other two progenies survival was 66 and 69%. This agrees with the results obtained in the previous experiment (Table 4), where two lines of hoppers (CC and DD) seemed to differ greatly in their susceptibility to the adverse effects of transovarially transmitted EWSM on *J. pellucida* nymphs.

Table 6. *Survival of nymphs and longevity of adults in outbred progenies* of Javesella pellucida, non-infective and congenitally infective with EWSM*

Treatment and progeny (line)	Initial no. of nymphs	Survival to adult (%)	Adult longevity (days)					
			Males			Females		
			Mean	S.E.	No.†	Mean	S.E.	No.†
Non-infective								
Progeny 1	59	96.6	30.0	2.47	20	49.9	2.64	34
Progeny 2	18	94.4	19.1	2.93	9	40.8	6.46	8
Progeny 3	90	91.1	17.3	1.71	40	35.9	2.65	43
Congenitally infective								
Progeny 1	48	97.9	15.6	1.50	19	36.3	3.45	28
Progeny 2	63	95.2	17.3	1.70	32	30.8	3.00	28
Progeny 3	64	68.8	23.1	3.94	12	36.0	2.55	32
Progeny 4	61	65.6	19.2	1.79	19	40.0	3.44	23

* Within each treatment, progenies are arranged in descending order according to their survival during the nymphal stage.

† No. of hoppers from which the information was obtained.

Counts of surviving nymphs every other day throughout the nymphal stage (Fig. 1) revealed that the greater mortality associated with inbreeding was apparent from the first day after hatching ($P < 0.001$), whereas the mortality associated with transovarially transmitted EWSM was negligible for 3 days after hatching. The latter mortality, however, was detectable in 5 to 9 day old nymphs ($P < 0.001$ on day 9), but was again negligible in older ones. Mortality associated with inherited EWSM thus occurred mainly in the second and early third nymphal stadia, whereas mortality associated with inbreeding occurred mainly during the first and fifth (last) nymphal stadia.

Duration of the nymphal stage was significantly longer in inbred hoppers than in outbred ones (Table 5, $P < 0.01$), but inherited EWSM had no effect in this respect. Males had significantly shorter nymphal duration than females ($P < 0.05$).

Adult longevity. In this experiment, the date of the final moult (emergence date) was known for each nymph that survived to adulthood. The mean emergence date

was calculated for each sex and experimental group separately. Since adults were reared in groups and counted weekly (Fig. 2), each adult was given a longevity score equivalent to the duration (in days) from day 0 (mean emergence date) and the mid-interval between the two counting dates preceding and following the death of this adult.

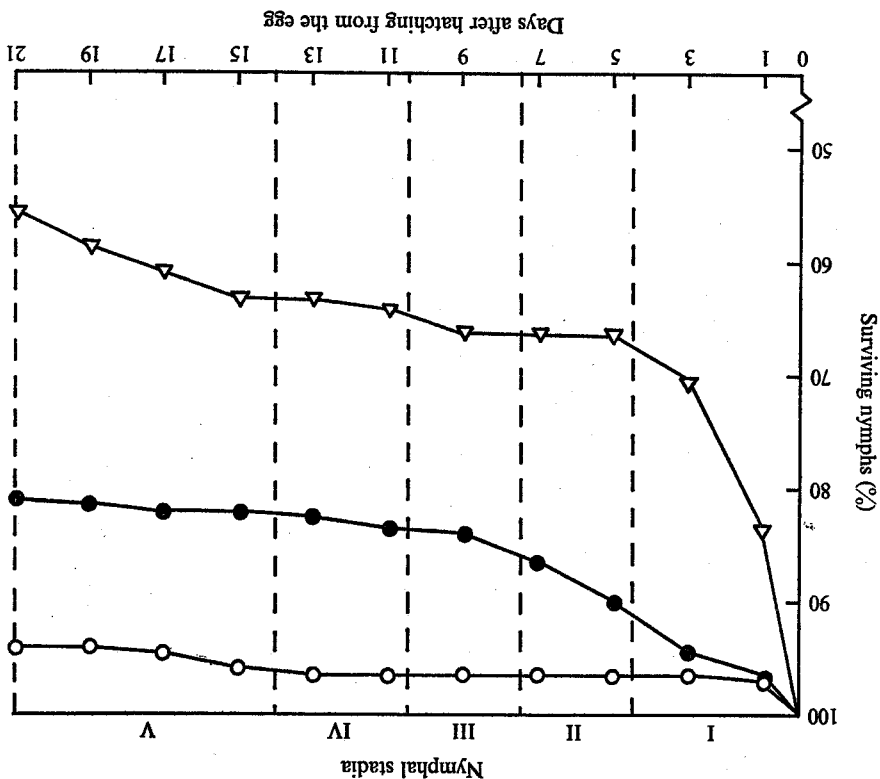


Fig. 1. Survival of *J. pellucida* hoppers throughout the nymphal stage. Parents of these hoppers were: Δ, non-infective inbred; ○, non-infective outbred; ●, congenitally infective outbred.

Females of *J. pellucida* lived significantly longer than males (Table 5, $P < 0.001$). Longevity of inbred adults of both sexes was one-third to one-half that of outbred ones ($P < 0.001$). Congenitally infective (outbred) adults of both sexes had a 14% shorter life span than non-infective outbred adults ($P > 0.01$). Within-treatment analyses of variance on the longevity of hoppers in the two outbred groups revealed significant differences ($P < 0.001$) between progenies of each group. The progenies of non-infective hoppers that survived best during the nymphal stage appeared to have lived longer as adults (Table 6). This trend may be explained in terms of genetic correlation between greater survival in the nymphal stage and longer duration in the adult stage (correlation coefficient in males, 0.87; in females, 0.96). In the congenitally infective hoppers, however, this trend is reversed: the two

progenies that survived best during the nymphal stage died sooner as adults (Table 6). It is possible that lines which are more susceptible to the adverse effects of inherited EWSM may be affected as nymphs, whereas more resistant lines may survive the nymphal stage but die earlier as adults.

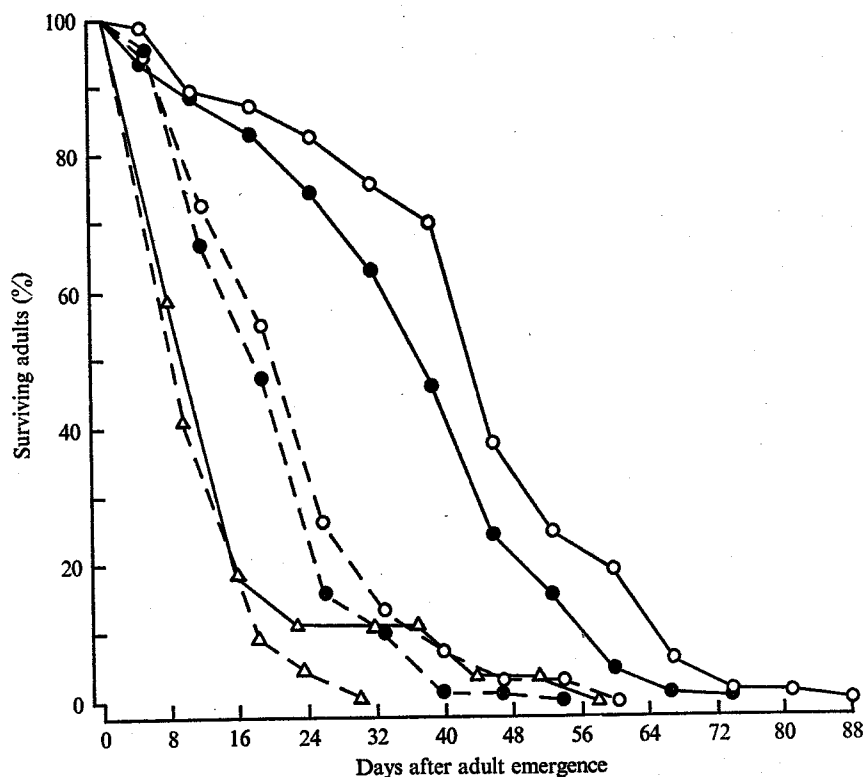


Fig. 2. Survival of adult *J. pellucida* males (----) and females (—), reared in groups and counted weekly. Parents of these hoppers were: Δ , non-infective inbred; \circ , non-infective outbred; \bullet , congenitally infective outbred.

DISCUSSION

The proportion of infective nymphs in the progenies of infective *J. pellucida* females ranged from 85 to 96%. Those nymphs that were infective within 7 days of hatching (71%) probably acquired EWSM transovarially, for its incubation period in vectors when acquired from diseased plants is at least 8 days (Slykhuis & Watson, 1958). Transovarial transmission to a similarly high proportion of individuals of the vector has been reported with rice stripe virus in *Laodelphax striatellus* Fallen (Yamada & Yamamoto, 1955) and with some other viruses and vectors (Carter, 1964).

European wheat striate mosaic, acquired transovarially, induced mild pathogenic effects on *J. pellucida* in the nymphal and adult stages but not in the egg stage. On the other hand, it has been shown previously (Ammar, 1975) that EWSM, acquired by first and second instar nymphs of *J. pellucida* fed on diseased plants, had no pathogenic effect on the survival of nymphs and adults of this vector.

Pathogenic effects on vectors of viruses and Mycoplasmas have been reported earlier (Jensen, 1963; Davis & Whitcomb, 1971), but to the author's knowledge, only one previous report states clearly that the pathogen has to be acquired transovarially, and not orally, in order to affect its vector; this report is on rice dwarf virus in its vector *Inasuma dorsalis* (Motsch.) (Shinkai, 1962). In the present work, it was found that the nymphal mortality associated with EWSM in *J. pellucida* occurred mainly in the second and early third nymphal stadia (5-9 days after hatching, at 19-22 °C). By this time, orally acquired EWSM would not have completed its incubation period in the vector (average of 14 days), and thus its concentration is expected to be relatively low. Therefore, it seems likely that in order to induce a pathogenic effect on *J. pellucida*, EWSM has to be established at a relatively high concentration in the tissues of the vector somewhat early in the nymphal stage, which can occur only when the disease is transmitted to the hoppers transovarially.

Certain lines of *J. pellucida* seemed to be more susceptible than others to the adverse effects of inherited EWSM (Tables 4, 6). Some lines, perhaps the more susceptible ones, are affected in the early nymphal stage, whereas others survive the nymphal stage but die earlier as adults (Table 6). It is possible that the pathogenic effects of EWSM on the eggs of *J. pellucida* reported by Watson & Sinha (1959) and by Sinha (1960) occurred in more susceptible lines of hoppers than those used in the present investigation.

Adverse effects of inbreeding on the embryos of *J. pellucida* have been reported earlier (Kisimoto & Watson, 1965), but further effects of inbreeding on the nymphal and adult stages of this species are reported in the present work. The effects of inbreeding on *J. pellucida* were much greater than those of inherited EWSM. This indicates the need for caution in designing and interpreting any experiments concerned with the effects of viruses and other pathogens on their vectors; lineage of the vector and the breeding system used have to be taken into consideration.

I am indebted to Dr P. W. Murphy and Mr J. Y. Ritchie for their helpful suggestions throughout this work, to Dr Marion Watson for her stimulating discussions and for providing the culture of EWSM, and to Dr R. T. Plumb (Rothamsted Experimental Station) for reading and criticizing the manuscript.

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