LONGEVITY, FECUNDITY AND EMBRYOGENESIS IN BRAZILIAN APHIDS[1]

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ABSTRACT - Aphids cause great damage to cultivated crops. With the aim of aid managing methods, biological properties subject to heavy selection were studied in the three south Brazilian species *Schizaphis graminum, Sitobion avenae* and *Rhopalosiphum padi* (Homoptera: Aphididae). Changes in embryonic outer morphology were analysed under contrast phase microscope and eight stages were described. The embryonic period terminated after 20, 24 and 26 hours; the longevity (expressed in number of days from nymph to adult death) was of 31.13±2.79, 29.73 ±1.5, 25.13 ±3.22 and the fecundity (number of nymphs per adult aphid) was of 66.87 ±8.05, 31.67 ±3.75, 49.53 ±6.26, respectively. When the fecundity/longevity ratio was compared it was concluded that *S. graminum* was the most dangerous to wheat, and BR-35 wheat strain was the most susceptible to aphid control. The differences in embryonic time and morphological characteristics can be used to classify the three species.

Index terms: *Schizaphis graminum, Sitobion avenae, Rhopalosiphum padi*, biological properties, insect pest control.

LONGEVIDADE, FECUNDIDADE E EMBRIOGÊNESE EM AFÍDEOS BRASILEIROS

RESUMO - Afídeos causam grande dano a cereais cultivados. Com o objetivo de subsidiar programas de controle, propriedades biológicas sujeitas a forte pressão de seleção foram estudadas nas espécies sul-brasileiras *Schizaphis graminum, Sitobion avenae* e *Rhopalosiphum padi* (Homoptera: Aphididae). Mudanças na morfologia externa dos embriões foram analisadas sob microscópio de contraste de fase, e oito estágios foram descritos. O período embrionário terminou com 20, 24 e 26 horas; a longevidade (expressa em número de dias desde ninfa até a morte do indivíduo adulto) foi de 31,13 ± 2,79; 29,73 ±1,5; 25,13 ± 3,22 e a fecundidade (número de ninfas por afídeo adulto) foi de 66,87 ± 8,05; 31,67 ±3,75; 49,53 ±6,26, respectivamente. Quando se comparou o quociente fecundidade/longevidade, concluiu-se ser *S. graminum* o mais prejudicial ao trigo, e a linhagem BR-35, a mais suscetível ao controle de afídeos. As diferenças no tempo e características morfológicas embrionárias podem ser usadas para classificar as três espécies.

Termos para indexação: *Schizaphis graminum, Sitobion avenae, Rhopalosiphum padi*, propriedades biológicas, controle de insetos-praga.

INTRODUCTION

Aphids are a problem in farming for a variety of reasons, but especially because of the devastating damage they cause to many crops cultivated by man. *S. graminum, S. avenae* and *R. padi* are three species of aphids that regularly infest cereal crops in winter in southern Brazil.

S. avenae and S. *graminum* were introduced into Brazil in 1966, and cause serious damage to the farming areas, probably due to absence of parasitoid control in this part of South America (Zuñiga, 1990).

R. padi is also one of the main cereal crop pests in Argentina, Brazil and Uruguay, at least since the 1930s (Costa & Müller, 1982). Few insects transmit viruses to the wheat as efficiently as these tiny, soft-bodied aphids. While feeding on the sap of wheat leaves, these insect pests can infest a crop with damaging viruses such as BYDV (Barley Yellow Dwarf Virus); their parthenogenetic viviparous reproduc-

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tion, combined with reduced generation time, enable populations to increase very rapidly (Dixon, 1985a, 1985b).

Reproduction of aphids is higher when temperatures are ideal, when monocultures of favoured host plants are grown, and, when these hosts are at their most nourishing developmental stage (Tatchell & Parkers, 1990). Frazer (1988) illustrated the astonishing reproductive capacity of the aphids as follows: "The progeny of one pea aphid fundatrix, if all survived, would exceed the mass of the earth by the end of summer". The conspicuous power of multiplication in the parthenogenetic phase of aphids is thus one of the main reasons why they are chief pests. They are considered "r" strategists, because r selection should clearly select for high reproductive potential (Pianka, 1970). The r selection results in the use of many resources which may possibly enhance fitness through increased reproductive output and enhanced fecundity and/or increased growth and somatic allocation for improved survival (Calow, 1979, 1982).

The objective of this work was to study the longevity, fecundity and embryogenesis of *Schizaphis graminum, Sitabion avenae* and *Rhopolosiphum padi* which are the most common aphid species in the southern states of Brazil.

MATERIAL AND METHODS

S. graminum, S. avenae and *R. padi* samples used in the present work were collected at the city of Passo Fundo, state of Rio Grande do Sul (Brazil) and maintained at the Embrapa Entomology Laboratory under standard conditions.The relative humidity of 65% and a photoperiod of twelve hours in special chambers (phytotron) were used for the three species, but *R. padi* was reared at 21°C, whereas 18°C was used for *S. avenae* and *S. graminum*.

Longevity and fecundity analysis

Seeds of BR-35 strain wheat were placed in 50 flowerpots for each apterous aphid species; when these plants were three centimeters high, they were infested with aphid nymphs. As soon as the wheat plant reached a height of 4 cm, or when the leaves turned yellow, the aphid was transferred to a new flowerpot with other 3 cm wheat plants. This procedure was performed until aphid death. The offspring were scored day by day. Longevity is defined here as the number of days from nymph to adult aphid death whereas fecundity expresses the number of nymphs per adult aphid. The results were statistically analysed by a Minitab Program (Minitab, 1989).

Embryogenesis analysis

The embryos of 30 apterous adults of each species were placed over a slide containing a drop of Petrolatum oil and immediately analysed under contrast phase Zeiss Microscope and photographed.

RESULTS AND DISCUSSION

Longevity

The average longevity of the aphids studied may be seen in Fig. 1. When analysing the longevity data of the three aphid species it was observed that *S. graminum* and *S. avenae* have a similar lifespan (31.13 ± 2.79 days and 29.73 ± 1.5 days) whereas *R. padi* lives only 25.13 ± 3.22 days.

Analysing the longevity data of the three aphid species it was observed that *S. graminum* and *S. avenae* have a similar lifespan whereas *R. padi* lives a shorter period. The only previous study regarding the lifespan of these same aphid species was performed by Gassen (1993) under the same temperature and humidity conditions but reared on another Brazilian wheat strain named CNT-10. As can be seen in Table 1, longevity was markedly different once *S. graminum* and *R. padi* increased their lifespan respectively by 11.8 and 7.6 days whereas *S. avenae* decreased this time by 6.2 days when the wheat strain used for aphid growth was changed.

Although it is very difficult to prove the difference in the quality of food provided by these two wheat strains, it is possible that, as stressed by Mittler (1958) and Dixon (1987), the aphids feeding on high quality food develop faster and become larger than those that feed on a poor quality trophic resource. In this sense, whereas CNT-10 is the best wheat strain for *S. avenae* development, because its longevity is increased, the opposite occurs for *S. graminum* and *R. padi* where lifespan increased on the BR-35 strain.

However, from the agricultural standpoint, as *S. graminum* and *R. padi* have less time to damage CNT-10, this strain could be recommended to farmer in localities where these aphid species occur. Nervertheless, the opposite will be recommended where *S. avenae* is found; here BR-35 is the better wheat strain since *S. avenae* longevity is shorter and thus has less time to infest the wheat plant.

Noda (1960) observed that *R. maidis* took 21.4 days to complete its development at 10°C and only 5.0 days at 25°C, whereas *R. prunifoliae* does the same in 4.7 days at 25°C. Our data on *R. padi* showed that the use of higher temperature decreased the lifespan. Furthermore the longevity between aphids reared in CNT-10 and BR-35 (Table 1) was also different. Thus these findings corroborate suggestions about the important role played not only by the quality of food but also by temperature in aphid developmental rate and longevity.

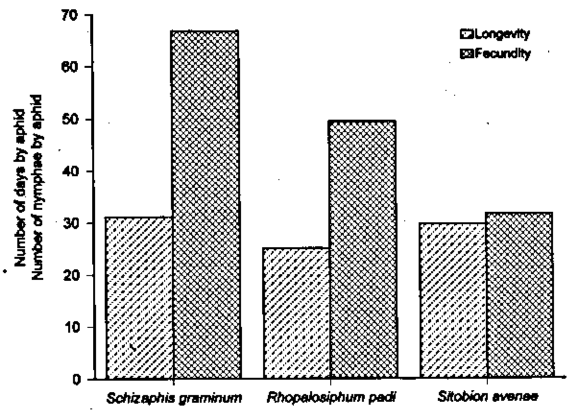

FIG. 1. Longevity and fecundity in three aphid species.

Fecundity

Results of the fecundity analysis which may be also observed in Fig. 1 showed that *S. graminum* produced 66.87 ± 8.05 nymphs per adult aphid, whereas *S. avenae* is less fecund, laying 31.67 ± 3.75 individuals. An intermediate mean fecundity value of 49.53 ± 6.26 was found for *R. padi*.

The data on fecundity revealed that *S. graminum* is by far the most prolific aphid species, laying twice the number of descendants as compared with *S. avenae*. Moreover, although having roughly a life span similar to *S. graminum*, *S. avenae* has a very small number of offspring. The comparison of the fecundity estimates between our data and those of Gassen (1993) given in Table 2, show that in all aphid species there was decrease in offspring when the BR-35 wheat strain was used.

TABLE 1. Comparative analysis of the longevity values obtained in *S. graminum*, *S. avenae* and *R. padi* in Gassen (1993) and in the present study.

Aphid species	Wheat strain	T (°C)	Longevity (in days ± S.D.[1])	Source
S. graminum	CNT-10	18	19.29 ± 1.69	Gassen (1993)
	BR-35	18	31.13 ± 2.79	Present study
S. avenae	CNT-10	18	35.91 ± 4.3	Gassen (1993)
	BR-35	18	29.73 ± 1.5	Present study
R. padi	CNT-10	21	17.5 ± 2.16	Gassen (1993)
	BR-35	21	25.13 ± 3.22	Present study

[1]S.D. = standard deviation.

TABLE 2. Comparative analysis of the fecundity values obtained in *S. graminum*, *S. avenae* and *R. padi* in Gassen (1993) and in the present study.

Aphid species	Wheat strain	T (°C)	Fecundity (nymph no. (S.D.[1])	Source
S. graminum	CNT-10	18	73.64 ± 3.82	Gassen (1993)
	BR-35	18	66.87 ± 8.05	Present study
S. avenae	CNT-10	18	40.07 ± 6.49	Gassen (1993)
	BR-35	18	31.67 ± 3.75	Present study
R. padi	CNT-10	21	41.29 ± 6.43	Gassen (1993)
	BR-35	21	49.53 ± 6.26	Present study

[1]S.D. = standard deviation.

These findings suggest that different strategies could be used by these species in order to assure their survival and escape from predators. Moreover, they provide strong support to the Blackman (1985) theory that the source of nutrition can be essential in regulating life parameters which are of undeniable importance to fitness.

Finally, when we compare the fecundity/longevity ratio obtained by us and by Gassen (1993) and shown in Table 3, one can observe that for all three species our results are lower. Therefore the aphid species reared in the BR-35 wheat strain studied in the present work are more susceptible to biological control, and among them *S. graminum* is the most dangerous to wheat.

Embryogenesis

During the embryonic development, profound modifications of each original form of aphid take place. Embryonic stages are defined by prominent features, easily distinguishable in the living embryo by direct observation or by immersion in any of several different media. Twenty, twenty four and twenty six hours were, respectively, the average time intervals for *S. graminum*, *S. avenae* and *R. padi* to reach the following ontogenetic stage.

By using external morphological changes, the embryonic period was tentatively divided into roughly eight stages described below for *S. graminum*.

First stage - The *S. graminum* embryo is egg-shaped and colourless, with two small brown spots at the blastoderm (Fig. 2a).

Second stage - A better definition of the whole body especially of the head of the aphid is observed. A certain amount of flexure and extension of the internal structures was also seen.

Third stage - A notable feature at this stage is the early development of the cephalic lobes. The eye primordia become discernible (Fig. 2b, 2c).

Fourth stage - Involves extension and flexure initially of the anterior end, and later of the caudal end. Considerable differentiation may be seen, especially of the spiracular tracheae (Fig. 2d, 2e).

Fifth stage - The differentiation continues, particularly of the spiracular tracheae, structures of the head and early thorax segmentation. At the same time the legs begin to develop (Fig. 2f). A process of head contraction and slackness takes place for a long period throughout the segmentation process.

Sixth stage - Anterior cephalic region movement is observed along the ventral side of the egg, until it arrives in its final position at the anterior pole; early development of antennal tubercules also occurs (Fig. 2g).

Seventh stage - In the developmental head area antennal tubercules may be seen in middle development, before the eyes become narrow; modifications occur at the middle of the head with the appearance of a sinuous border; re-entering and reliefs can be seen and at this stage, sinuous legs and siphunculi can be observed.

Eighth stage - An outline of proboscis is seen in the head, the cauda is less developed than the siphunculi. At this stage a new embryo can be observed inside the developing embryo. Wood & Stark (1975) designate this phenomenon as paedogenesis or reproduction at a sexually imature stage. At this time the thorax, which had an amorphous feature, becomes more conspicuous, spiracular tracheae show active movements of dilatation and slackness. Antennal tubercules are highly developed and antennal segments begin to develop. The legs may be clearly seen (Fig. 2h).

TABLE 3. Comparisons among the quocients of fecundity/total longevity estimated for *R. padi*, *S. graminum* and *S. avenae* in the present study and those of Gassen (1993).

Source	Wheat strain	*R. padi*	*S. graminum*	*S. avenae*
Gassen	CNT-10	2.36	2.29	1.12
Present study	BR-35	0.97	2.14	1.07

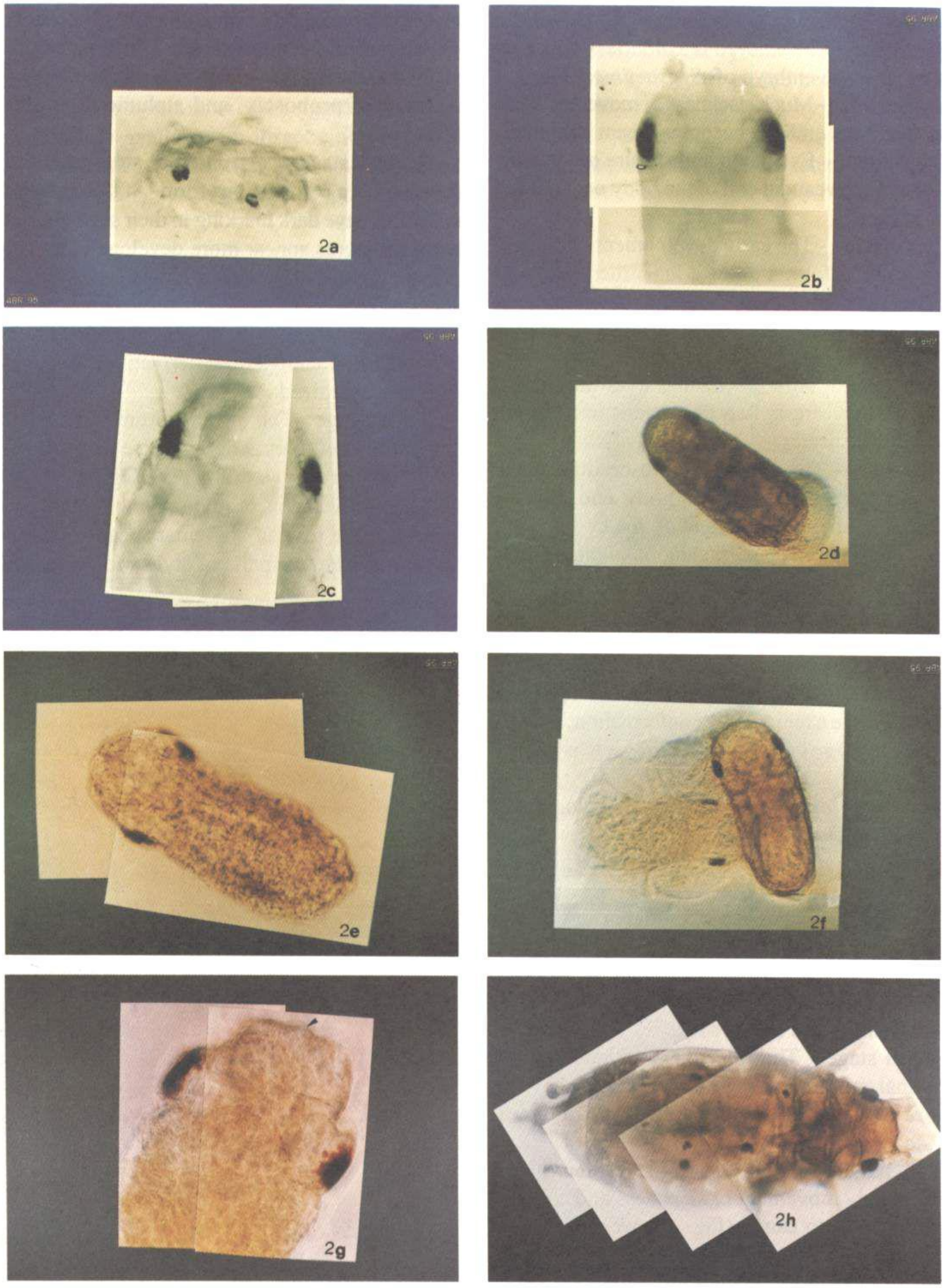

FIG. 2. Embryonic phases of *Schizaphis graminum*.

For *Sitobion avenae*, the following features were observed:

First stage - The embryo is colourless and egg--shaped as is the embryo of *S. graminum*.

Second stage - Much slackness of movements can be seen and the embryo becomes cream coloured.

Third stage - Extension and flexure of the anterior end and the caudal end of the body occur at this point in time.

Fourth stage - The early development of the proboscis and the formation of a leg structure can be observed and the whole body has many sinuous borders that will be the future body segmentation and the cauda (Fig. 3a).

Fifth stage - This species has eyes during this stage, but they are not so characteristic as in the *S. graminum* species.

Sixth stage - The eyes and proboscis differentiation are high in the anterior body end and the siphunculi in the posterior end of the body.

Seventh stage - The segmentation of the thoracic part can be more clearly observed, the legs are more developed; internal head structures conformation and stylets are more conspicuous; the development of legs and eyes may also be seen (Fig. 3b).

Eighth stage - The legs are well developed, the siphunculi have a remarkable conformation, as compared with *S. graminum*. The proboscis is clearly visible.

For *Rhopalosiphum padi* the embryogenesis shows the following main features:

First stage - The embryo is colourless, but the eye pigmentation is visible (Fig. 4a).

Second stage - Involves the initial extension and flexure of the anterior end and then the caudal end, with some differentiation of the spiracular traqueae.

Third stage - Early siphunculi and legs development can be seen (Fig. 4b).

Fourth stage - The joint differentiation of the abdominal and thoracic segments occurs along with a more noticeable development of siphunculi (Fig. 4c).

Fifth stage - Higher caudal development and constant body movement of slackness and contraction from head to cauda (Fig. 4d) were observed. The eyes are bigger and proboscis differentiation at the anterior body end, besides the differentiation of siphunculi at the posterior body end, occur.

Sixth stage - Eyes with greater development and identification of the ommatidia can be observed. The stomach contents with small differentiation, are visible, as well as the projection of cauda, the constitution of proboscis and siphunculi structures (Fig. 4e).

Seventh stage - All internal structures can be observed in a conspicuous form. At this stage some structures have dark marking in their segments; other body structures appear more developed, they have morphologically defined segments, as to pattern elements. They contain segments that are probably constituted by derivatives of the mesoderm and ectoderm, while endodermal derivatives are not segmentally organized.

Eighth stage - The clypeolabrum becomes thinner and begin to retract giving rise to a conspicuous triangular gap ventrally. The legs are fully developed. Movements of midgut and hindgut can be observed. We saw an alimentary canal composed by four stylets: two pairs of stylets forming the ex-

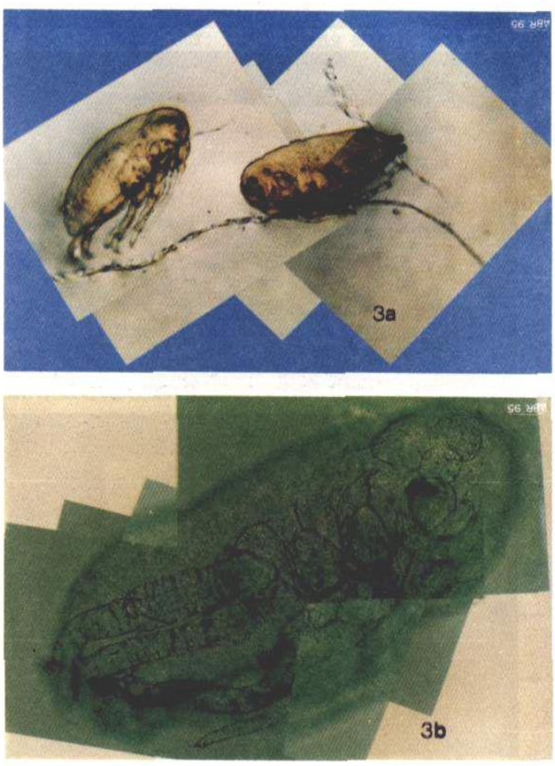

FIG. 3. Embryonic phases of *Sitobion avenae*.

ternal mandible, and the other two pairs forming the maxila. Both of them constitute an alimentary tract and a small salivary canal.

Among the insects, *Drosophila* is the paradigm organism that provides most of the significant knowledge presently available on insect embryogenesis and developmental genetics. The developmental biology of aphids, however, remains poorly understood. Several handicaps contribute to prevent the success of any attempt. For instance, Blackman (1985) stresses that the type of food supply is important in the embryonic period because the development as a whole is affected by the nutrients in each of the different stages. He also emphasizes the role of maternal control in the rate of embryogenesis and in the number of future offspring develop-

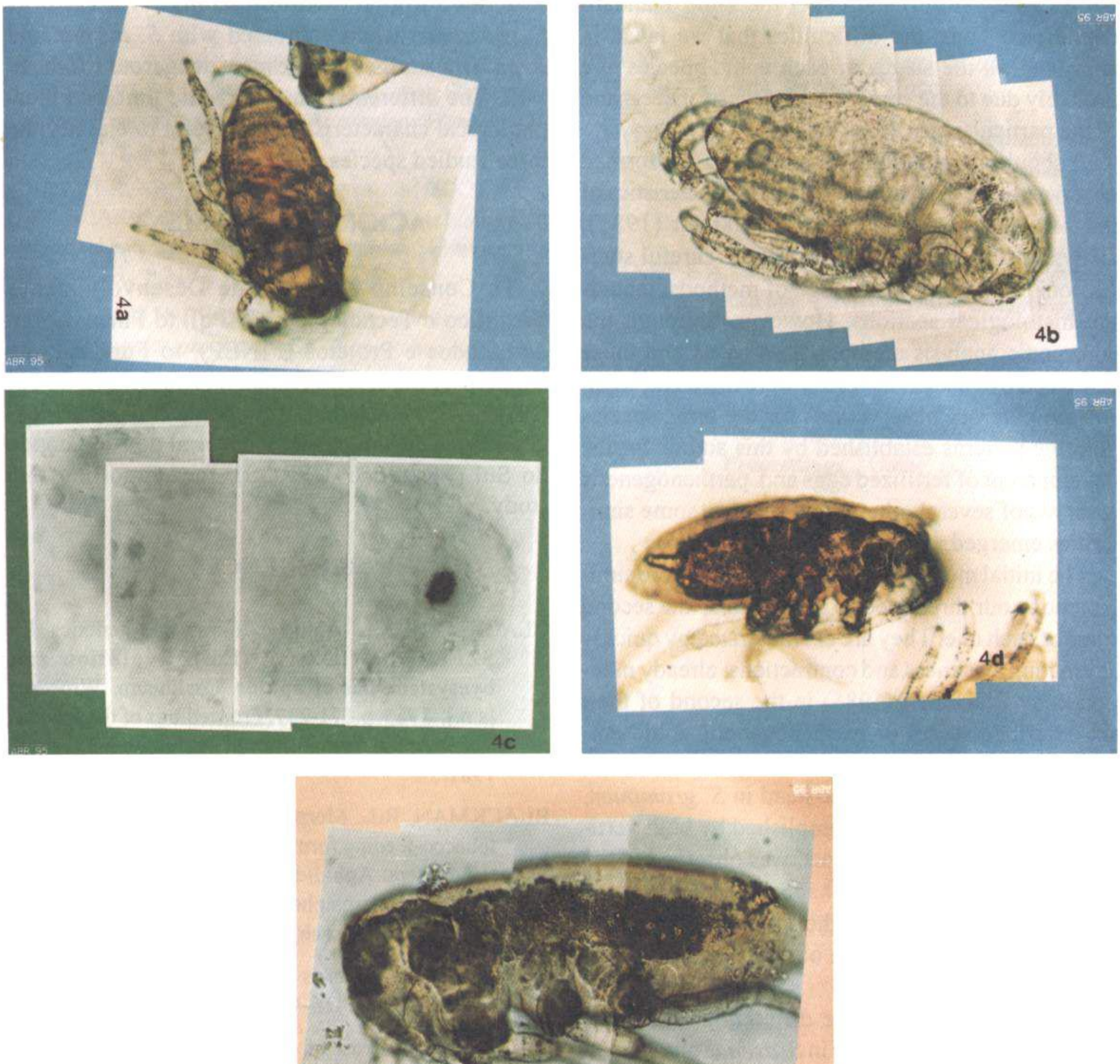

FIG. 4. Embryonic phases of *Rhopalosiphum padi*.

ment. Dixon (1987) also adds the paramount role of temperature besides nutrition in duration of development, survival and offspring production.

A clear description of the embryogenesis of *S. avenae*, *S. graminum* and *R. padi* could not yet be fully provided, although the constraints imposed by nutrition were overcome by our controlled experimental conditions. To avoid this type of problem, we kept all our samples in a same host plant (the BR-35 wheat strain) and under the same standard conditions. Thus, the difficulties that we faced in analysing all the stages of each aphid species, are probably due to the complexity of these insects and to the particularities of each one.

It should be mentioned that we only performed observations on the morphological characteristics of the whole embryos, whereas Blackman (1985), analysing other aphid species, made careful studies consisting of a broad range of methods, including histological sections. However, although the embryonic analysis methods used by us and those described by Blackman (1987) were different, when we compare our observations for the three species with the patterns established by this author for the development of fertilized eggs and parthenogenetic embryos of several other aphid species, some similarities emerged.

The initial morphogenetic movements were similar among our three species and begin at the second stage of each one. They are characterized by quickly alternating slackness and contractions, already mentioned by Blackman (1985) in the second of their six described stages of parthenogenetic aphid embryos.

The differentiation of the head in *S. graminum*, *R. padi* and *S. avenae*, accomplished by both vertical and horizontal movements, was observed in the fifth stage of the two former species and in the seventh of the later one. In the study of Blackman (1985), head differentiation occurs also in the fifth stage.

In *S. graminum*, the eye differentiation occurs during the seventh stage but in *S. avenae* and *R. padi* this fact occurs in the fifth stage, as described by Blackman (1985).

The occurrence of a small group of cells later in the posterior pole of the egg, which is responsible for the future formation of a "polar organ", as referred by Blackman (1985) with *S. graminum* was not confirmed in our study.

CONCLUSIONS

1. The lower fecundity/longevity ratio of the aphids in BR-35 wheat strain makes it the most susceptible to aphid control.

2. The higher fecundity/longevity ratio of *S. graminum* when compared with *S. avenae* and *R. padi* means that it is the most dangerous to wheat.

3. The differences in embryonic time and morphological characteristics are useful to classify the three studied species.

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