STUDIES ON THE ACTIVE FORM OF CALLOSOBRUCHUS MACULATUS (F.) IN NIGERIA

III. THE DYNAMICS OF ACTIVE FEMALE PRODUCTION IN CALLOSOBRUCHUS MACULATUS (F.) (COLEOPTERA, BRUCHIDAE) IN STORED COWPEAS

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INTRODUCTION: The bruchid, *Callosobruchus maculatus* (F.), commonly known as the cowpea weevil, is an important field-to-store pest of cowpeas (*Vigna unguiculata* Walp.) and other tropical grain legumes. *C. maculatus* damage at harvest is usually less than 10 per cent but infestation builds up rapidly in storage and 37 - 60% of the seeds may exhibit emergence holes within 4 - 6 months of storage. Losses in weight and quality are considerable under unimproved conditions of storage common in developing countries for cowpeas and Caswell [1] in 1968 estimated an annual weight loss of 24,000 tons valued at 0.84 million for Nigeria. At present day production figures of about 1 million tons the annual weight loss due to Bruchid damage would be of the order of 30,000 tons and at an enhanced value of £2.1 million (₦4.2 million). Comparable or higher levels of losses also occur in nearly all other developing countries of Africa.

Utida [2] was the first to describe, from Japan, a type of polymorphism in *C. maculatus*. He identified an abnormal form which he referred to as the 'flight' or distributive form and distinguished it from the normal, neotenic or flightless form [3, 4]. Caswell [5] reported a similar form from Nigeria and described it as an 'active' form. Utida [6] summarised the main characteristics of this form and the major factors associated with its production. Taylor [7,8] showed that the normal form, contrary to what had been assumed by previous authors, was capable of flight and that field infestation was due to both normal and active forms although the field populations studied over four planting seasons were predominantly of the 'active' form, presumably because of its greater flight activity. Utida [6], and Sano [9] discussed the significance of the active form and suggested that it was probably a more primitive adult form. Taylor [8], however, felt that the active form has arisen from the normal form and its main significance is that it provides a mechanism for dispersal from high population densities in heavily-infested stored cowpeas to uninfested stored legume seeds or mature legumes in the field.

During storage, both forms are produced and although Taylor [8] showed that 'active' female production increased with increases in initial population densities in culture and Sano [9] using heaped beans (*Phaseolus radiatus aureus*), demonstrated the dominance of temperature effect in the production of active forms, the dynamics of active form production in *C. maculatus* infested cowpeas stored under normal store-house conditions in jute sacks is imperfectly understood. Very little is also known of how this and other factors influence the progress and degree of infestation and the final index of damage at the end of the storage period. These aspects are of considerable importance in view of the significant physiological and reproductive differences between the two forms, especially the remarkable longevity and low fecundity of the active female [6]. This paper describes a study of the dynamics of active female production in cultures in the laboratory and in field-infested cowpeas obtained locally and stored in small sacks under conditions similar to cowpea storage conditions commonly found in most parts of the tropics.

MATERIALS AND METHODS: A series of three experiments was conducted to further elucidate the dynamics of active female production.

In Experiment I, observations were made on the production of 'active' females in cultures of *C. maculatus* with a predetermined initial population of males and females on 200 g of uninfested seed maintained in the laboratory. The whiteseeded, rough-coated variety of cowpea ('Mala') used in this experiment had been stored hermetically for a period of two months and only uniform seeds which had no eggs and no exit holes were selected. 200 g of such seeds at a moisture content of 5% were placed in 3 lb Kilner jars and 5 each of newly-emerged males and normal females were introduced. A total of 20 such jars were set up and held in a climatic cabinet at 27°C and 60% R.H. At 6 weeks, and subsequently every 2 weeks until 14 weeks, 4 jars were removed and the contents analysed for males, normal and active females, and damage index.

In Experiment II, attempts were made to simulate local storage conditions in jute sacks by placing 900 g each of a white-seeded cowpea purchased from the local market at the beginning of the storage season in December in specially sewn small bags made out of jute sacks. The seeds were thoroughly mixed before weighing and no insects were introduced into the sacks, except for the fact that all locally-produced cowpeas normally suffer from a level of pre-harvest infestation by *C. maculatus*. Twenty-four of such bags were placed on wooden slats on a shelf in a storage in which the temperature fluctuated between 26° and 29°C and the relative humidity between 60 and 80%. The contents of 4 each of the bags were analysed as in Expt. I after 4, 8, 12, 16, 20 and 24 weeks; the total period of storage being ca. 6 months.

A similar set of 4 jute bags was set up in the same storage for Expt. III. These bags were, however, taken out every 2 weeks and the contents sieved through a 4 mm mesh sieve to remove the insects. The insects so removed were analysed as in the previous experiments but the seeds were placed back in the bags which were then resewn and replaced in the store. This procedure to a certain extent simulated the physical removal of insects from infested cowpeas commonly practised by local dealers in the attempt to offer apparently insect-free cowpeas for sale and to some extent the escape of insects from infested sacks of cowpeas which is common under local storage conditions and is often the source of cross-infestation and pre-harvest infestation of *C. maculatus*.

RESULTS: The results of Experiments I - II are presented in Tables I - III and Fig. I. In Experiment I with a starting population of 5 males and 5 normal females the progeny at 6 weeks (one generation) gave an active/normal female ratio of 1:2. This ratio declined significantly to 1:1.4 at 8 weeks (2 generations) and continued to decline until it reached the lowest point of 1:0.2 at 12 weeks. It a-pears that after the lowest ratio of normal females the proportion of normal females began to increase, giving a ratio of 1:0.4 at 14 weeks; this trend is confirmed by the data in Table II where observations were continued in the jute sack for 24 weeks. The yield of progeny was high initially with a factor of ca. 79 after the first generation (6 weeks) but yields of progeny were below the expected figures for subsequent observations and generations probably due to the effect of population density, mutual interference, lower egg viability and egg and larval mortality (Utida [6]).

The damage index shown as percentage damaged seeds (seeds with exit holes) (Table I) increased significantly from 22% after six weeks to about 43% at 10 weeks. Although the percentages of damaged seeds recorded when the infested seeds were analysed at 12 and 14 weeks were slightly lower than the highest damage index at 10 weeks they were not significantly different. Also it appears that the high population densities in cultures at these stages caused greater egg and larval mortality and reduced the numbers of adults which emerged successfully. The male/female ratio remained ca. 1:1 for the first ten weeks but declined to 1:0.7 and 1:0.6 at 12 and 14 weeks, indicating that as the cultures became older and the population density increased there was a tendency for more males to be produced. Males are normally smaller in size and probably have a greater chance of developing successfully into adults under these conditions of fairly intense competition in the breeding medium.

The development of bruchid infestation in naturally infested local cowpeas bagged in small jute sacks was slow initially with only 469 adults produced in 908 g of seed and a damage index of 19.3% after 12 weeks. There was a preponderance of normal females in the adults which emerged during the early stage of storage in sacks and the ratio of active/normal females remained at about 1:5 for the first three observations at 4, 8 and 12 weeks. However, between 12 and 16 weeks of storage (approximately 4 generations) there was a sharp rise in the ratio of active females and a ratio of 1:0.5 was attained at 16 weeks. This represents the peak of the production of active females as subsequent analysis showed an upward trend of the incidence of normal females (Table II) and the ratio of active/normal females at the end of the experiment (24

TABLE I: The production of 'active' females of C. maculatus in continuous cultures in the laboratory for $3\frac{1}{2}$ months (14 weeks). Starting population 5 normal females and 5 males on 200 g of seed.

Period of storage	Yield of progeny	*Mean no. of adults	Mean no. of males	Mean no. of active females	Mean no. of normal females	Ratio of active: normal females	Male/Female Ratio	Percentage damaged seeds
6 weeks	x78.8	788	440	114	235	1 : 2.1	1 : 0.8	22.2
8 weeks	x95.2	952	500	187	266	1 : 1.4	1 : 0.9	22.5
10 weeks	x288.4	2884	1517	856	512	1 : 0.6	1 : 0.9	45.5
12 weeks	x367.5	3675	2122	1278	275	1 : 0.2	1 : 0.7	41.1
14 weeks	x457.1	4571	2806	1253	512	1 : 0.4	1 : 0.6	39.7

TABLE II: The production of 'active' females of C. maculatus in small sacks of cowpea in storage over a period of six months (24 weeks).

Period of storage	*Mean no. of adults	Mean no. of males	Mean no. of active females	Mean no. of normal females	Ratio of active: normal females	Male/ Female Ratio	Percentage damaged seeds
4 weeks	54	41	2	10	1 : 5	1:0.3	2.2
8 weeks	55	48	1	5	1 : 5	1:0.1	2.5
12 weeks	469	197	44	226	1 : 5.1	1:1.4	19.3
16 weeks	4480	2451	1321	700	1 : 0.5	1:0.8	64.1
20 weeks	4393	2771	736	815	1 : 1.1	1:0.8	72.4
24 weeks	6570n	3642	1084	1577	1 : 1.5	1:0.7	90.1

*Mean of 4 replicates.

TABLE III: The production of 'active' females of _C. maculatus_ in small sacks of stored cowpea sieved every two weeks for a period of six months (28 weeks)*

Period of storage	**Mean no. of adults	Mean no. of males	Mean no. of active females	Mean no. of normal females	Ratio of active: normal female	Male/ Female Ratio	_B. atrolineatus_
2 weeks	37	33	2	2	1:1.0	1:0.1	2
4 weeks	10	8	1	1	1:1.0	1:0.3	0.3
6 weeks	28	13	1	14	1:14.0	1:1.1	0.5
8 weeks	202	92	5	105	1:21.0	1:1.2	0.3
10 weeks	397	176	30	191	1:6:4	1:1.3	-
12 weeks	1011	434	236	341	1:1.4	1:1.3	-
14 weeks	1085	612	215	258	1:1.2	1:0.8	-
16 weeks	996	544	224	228	1:1.0	1:0.8	-
18 weeks	1966	1168	348	450	1:1.3	1:0.7	-
20 weeks	1598	933	293	372	1:1.3	1:0.7	-
22 weeks	521	331	75	115	1:1.5	1:0.6	-
24 weeks	172	103	35	34	1:1.0	1:0.7	-
26 weeks	62	37	10	15	1:1.5	1:0.7	-
28 weeks	53	33	8	12	1:1.5	1:0.6	-
Total	8138	4517	1483	2138	1:1.4	1:0.8	3.1

*Damage index at 28 weeks was 62%.

**Mean of 4 replicate sacks.

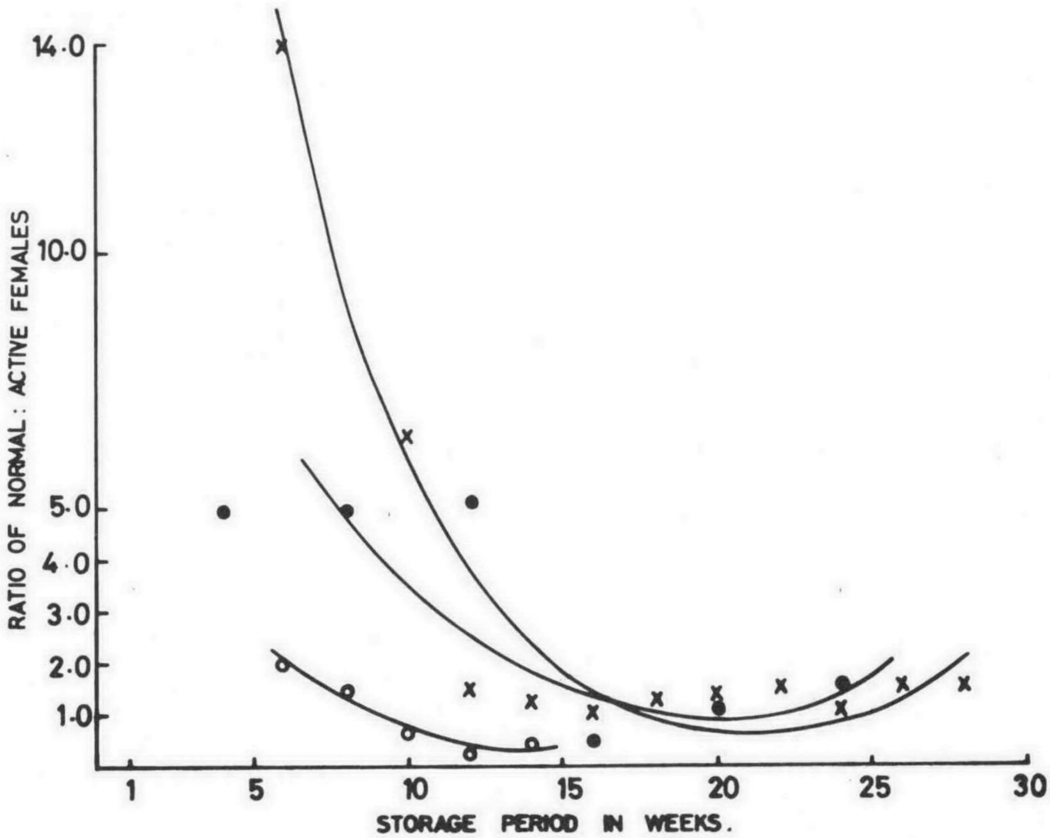

FIGURE 1. The relationship between the ratio of normal/active females and the period of storage in cowpea. (o = Expt. I; = Expt. II; x = Expt. III).

weeks) was 1:1.3. These results indicate that the peak of active female production and therefore the peak period of dispersal from sites for cowpea storage can normally be expected to occur about 4 months after the commencement of storage. The damage index after 4 weeks of storage agreed with the 2% level of field infestation recorded by Booker [11] but damage increased dramatically during the 24 weeks of storage and the final damage index was about 90%.

Table III gives the data for the incidence of active and normal females of *C. maculatus* in Expt. III in which the contents of the small jute sacks were sieved every two weeks and the insects recovered analysed. The initial infestation was even lower than in Experiment II and meaningful number of bruchids were not recorded until the 6th and 8th weeks. The proportion of active females to normal females was initially varying from 1:6 to 1:21. This proportion continued to increase until it came at par with that of normal females at 16 weeks (ca. 4 months). Subsequent determinations continued to show increases in the normal female proportion varying from 1:1.3 to 1:1.5, except that the ratio was about 1:1 again at 24 weeks. There was, however, a steady decline in the numbers of adult bruchids recovered from the infested cowpeas from 22 weeks onwards and the numbers per bag at 28 weeks was only 53 made up predominantly of males. The male/female ratio fluctuated between 1:0.6 and 1:1.3 during the period from 6-28 weeks but was initially close to unity. It also appears that more males were produced as the period of storage advanced and more adults were produced. It is remarkable that the highest ratio of active to normal females also occurred 16 weeks after the commencement of storage although the actual peak number of active females was recorded two weeks later. This indicates that the periodic removal of adults by sieving had little or no influence on the timing of the production of active females. It, however, had a marked effect on the total number of adult bruchids that bred successfully in the samples of cowpeas and reduced the index of damage which was found to be about 62% after 28 weeks storage.

Another bruchid, *Bruchidius atrolineatus* (Pic.) was recorded from the sieved insects but in very low numbers and only during the first 8 weeks of the experiment (Table III). Although pre-harvest infestation of cowpea by this species is known to occur in Nigeria, Prevett [10] had shown that it does not persist as a pest in stored cowpeas and the present observations confirm this. Booker [11] concluded that this was partly due to a much reduced level of egg production and a mean developmental period and a period of emergence which are longer than those of *C. maculatus*.

DISCUSSION: The dynamics of active female production in *C. maculatus* indicated by the results of these experiments suggest that the type of polymorphism exhibited by this species bears a definite relationship to and may have evolved as a result of storage conditions. There is a clear indication that the proportion of active females increases with the length of storage and usually reaches a peak in relation to normal females about 16 weeks (4 months) after the commencement of storage in field-infested cowpeas. In cowpeas which were artificially infested and maintained in the laboratory the same effect was demonstrated although it would appear that the ratio of 5 females to 200 g of seed was higher than normal levels of field infestation, thereby resulting in an active/normal female ratio substantially lower than 1:1 at 10 weeks of infestation.

The factors inducing the production of active forms in *C. maculatus* have been discussed by Sano [9], Utida [6] and Taylor [8]. The present results seem to uphold the suggestion by Taylor [8] that active females as flight or distributive forms would be expected to be produced in larger numbers when infesting populations are faced with the need to disperse. This appears to be the situation when infested cowpeas have been in storage without fumigation for about 4 months. Under the conditions of these experiments which simulate normal storage conditions on a small scale, the progressive increase in the proportion of active to normal females from 10 weeks after the commencement of storage to a peak at the 16th - 18th weeks appears to be related to the build-up of insect populations in the medium, temperature and the need for a dispersal mechanism. Even when insects were removed by sieving every two weeks the highest ratio of active/normal females was attained after approximately the same period.

It would appear that after about 4 months of storage there is a reverse trend in the production of active females. This may be due to the loss of active females which in an attempt to escape were often found in large numbers on the walls of stores containing infested cowpeas [7]. It may also be due to the fact that active females have so far been observed to produce only normal females, lending support to the views by Caswell [5] and Utida [6] who felt that a genetic factor or hereditary element was involved. If such a factor was indeed involved it would appear to be triggered off at a susceptible larval stage (Sano [9])and by high population densities and high temperature both of which seem to operate in heavily-infested seed about 16 weeks after the commencement of storage. The normal form factor would be expected to be dominant as copulation between normal males and active females always produced normal adults; the gonads of active males are known to be undeveloped.

The dynamics of active form production in cowpeas stored under normal storage conditions in bags confirm the hypothesis that this type of polymorphism in *C. maculatus* principally arose as a mechanism for dispersal as the population builds up on infested cowpeas in storage (Taylor [8]). The greater flight activity, greater longevity, higher fat body contents and delayed oviposition of the active female (Utida [6]) confer greater success on it as a dispersal agent and source of cross-infestation and pre-harvest infestation. It now seems clear also that the high incidence of the active form observed by Caswell [5] in April to May in southern Nigeria is probably not related to the ambient conditions of temperature, humidity and seed moisture content but to the peak of active form production in cowpeas which have been in storage for 16 weeks or more since harvesting in December or early January. The market samples of cowpeas from which Prevett [10] observed greatest numbers of active forms after 6 - 10 months of storage have probably been stored unshelled as is the traditional practice in which case the development of infestation was slow and the peak incidence of active forms delayed.

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