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SUMMARY

1. A three-year survey revealed that infestations of *Trogoderma glabrum* (Herbst) are well established in grain storages in 43 Nebraska counties.

2. Egg development required an average of 11.5 days at 70°, 7.7 days at 80°, 5.9 days at 90°, and 4.3 days at 100° F. No eggs hatched at 60° F.

3. Larvae fed mainly on the germ portion of kernels. Feeding occurred on the endosperm and bran portions only after the germ had been consumed. Larvae penetrated only the top two or three feet of stored grain.

4. At 90° F. larvae developing into females on whole wheat germ and flour molted five or six times, larvae developing into males molted four or five times. Under adverse conditions larvae molted 11 or 12 times.

5. With a diet favorable to growth, larvae completed their development in approximately 139 days at 70°, 39 days at 80°, and 25 days at 90° F.

6. First instar larvae attacked sound whole wheat kernels containing 15 percent moisture. Although larval development was delayed on whole wheat, survival was equal to that on whole wheat flour. The increase in time necessary for larval development on whole wheat was not associated with the ultimate sex of the larvae.

7. The time necessary for larval development and the rate of larval survival was a function of the number of larvae per unit grain mass and the amount of cracked wheat or corn in that mass. The amount of cracked grain in a mass of corn or wheat determined size of population. The moisture content of the wheat within the limits of 12 to 15 percent did not influence larval development and survival. Larval survival, particularly of larvae developing into females, was materially reduced on corn with a 12 percent moisture content.

8. *T. glabrum* was able to complete its development on sorghum.

9. Newly-hatched larvae survived at 36° F. for 13 days, but 40 percent died after 20 days and all were dead after 50 days. At 60° F., 30 percent were alive after 150 days.

10. Larvae survived starvation for several months.

11. A protozoan pathogen belonging to the *Mattesia* group was very common in *T. glabrum* cultures.

12. The pupal period, spent in the last larval skin, ranged from about eight days at 70° to about three days at 100° F.

13. Exposure to 36° F. for about two weeks was fatal to all pupae.

14. Newly-emerged adults spent a quiescent period in the last larval skin. The quiescent period varied from about seven days at 70° to about two days at 100° F.

15. Adults mated immediately after leaving the last larval skin. The preoviposition period varied from two to three days at 70° to one day at 90° and 100° F. Peak egg production, 92 eggs per female, occurred at 80° F.

16. *T. glabrum* adults did not feed. Longevity of both males and females decreased with an increase in temperature, but unmated males and females survived longer than mated adults. Longevity ranged from 3 days at 100° to 50 days at 70° F.

17. The average time required to complete the life cycle was 50.6 days on whole wheat at 90° F. and 65 to 70 percent relative humidity.

18. *T. glabrum* overwinters in the larval stage in Nebraska.

19. Several species of *Aspergillus* survived passage through larvae, pupae, and adults of *T. glabrum*. These included *Aspergillus repens* (Cda.) DeBary, *A. chevalieri* (Mangin) Thom and Church, *A. ruber* (Bremer) Thom and Church, *A. restrictus* Smith, *A. amstelodami* (Mangin) Thom and Church, *A. flavus* Link, *A. candidus* Link, *A. ochraceus* Wilhelm, and *A. niger* van Tieghem.

The Biology and Ecology of *Trogoderma glabrum* (Herbst) in Stored Grains

Benjamin H. Kantack and Robert Staples[1]

INTRODUCTION

These investigations were undertaken to determine the distribution and importance of *Trogoderma glabrum* (Herbst) in stored grain in Nebraska, the ecological factors favoring population increase in stored wheat, corn, and sorghum, and the role *T. glabrum* might play in disseminating internally the *Aspergillus* molds commonly encountered in stored grain.

Literature Review

Several species of dermestid beetles have been recorded as pests of stored grain throughout the world. However, it was not until after

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the discovery of the Khapra beetle, *Trogoderma granarium* Everts, in California by Allen and Linsley in 1954, that entomologists started to focus their attention on species occurring in the United States.

Trogoderma glabrum was first recorded in Nebraska in March 1956 when C. J. Walstrom, State Entomologist, found a single larva in Lincoln on brome grass seed (Fitchett, 1960). This species has been recorded in the United States in Colorado, Idaho, Illinois, Iowa, Kansas, Minnesota, Missouri, Oregon, Washington, Wyoming, California, South Dakota, and Texas (Beal, 1956; McGregor, 1958; Bezant, 1956). *T. glabrum* has been found in cottonseed meal, barley, corn, wheat, soybean meal, wheat bran, mud dauber nests, nests of *Odynerus* and *Osmia*, and nests of the English and eastern field sparrows (Bezant, 1956; Strom *et al.*, 1959; Beal, 1954; Linsley, 1942, 1944; Hicks, 1953).

Aside from a few limited observations by Beal (1956) who reported that several generations of this species were maintained on yellow cornmeal and some observations by White and McGregor (1957) on a severe infestation of *T. glabrum* in stored wheat and corn in Kansas, details on the biology and ecology of this species are unknown.

Christensen (1957) stated that the principal stored-grain fungi belong to the genera *Aspergillus* and *Penicillium*. Members of the *Aspergillus glaucus* "group species" are able to invade stored seeds at moisture contents encountered in storage.

This group is divided into nine series. Four series, those typified by *A. amstelodami* (Mangin) Thom and Church, *A. ruber* (Bremer) Thom and Church, *A. restrictus* Smith, and *A. repens* (Cda.) DeBary, include the major fungi causing deterioration of wheat at moisture levels below 15 percent. With increasing moisture content above 15 percent, *A. flavus* Link ex Fries, *A. versicolor* (Vuill.) Tiraboschi, *A. tamarii* Kita, *A. ochraceus* Wilhelm, and *A. candidus* Link appear, all of which are damaging to stored cereals.

Agrawal *et al.* (1957, 1958) associated several species of *Aspergillus* with the granary weevil, *Sitophilus granarius* (L.). *A. restrictus, A. repens, A. ruber,* and *A. amstelodami* were isolated from infected grain on which weevils were feeding. Fungi were found in the digestive tract of *S. granarium*. Agrawal *et al.* (1957, 1958) and Christensen and Hodson (1960) showed that the granary weevil disseminated fungi in stored grain. Fungal infections in the grain favored development of weevil infestations. Similar results were obtained by Griffiths *et al.* (1959) with two species of mites, *Acarus siro* L. and *Tyrophagus castellanii* Hirst. Mites were vectors of storage fungi and carried these molds readily to new infection courts. Van Wyk *et al.* (1959) found that the confused flour beetle, *Tribolium confusum* Duval, caused a reduction in storage molds. This was attributed to volatile quinones secreted by the adult beetles. The presence of molds favored *Tribolium confusum* as more adult beetles survived on infected grain.

Distribution of *Trogoderma glabrum* (Herbst) in Nebraska

During October through December of 1958, 1959, and 1960, samples were withdrawn from wheat and corn storages throughout Nebraska. Samples were obtained from grains stored for at least one year in bins sealed under the Commodity Credit Corporation.

The standard U.S.D.A. sampling technique was used. This consisted of probing one or more samples at a depth of five feet in each quadrant and center of the bin. These samples were mixed and 1000 grams of the composite sample examined by sifting through official grain dockage sieves. Visual observations were made on all samples after sifting.

In 1958, 39 percent of the 256 wheat bins examined were infested with *T. glabrum* larvae or adults. In 1959, 5.9 percent of the 117 bins examined were infested, and in 1960, 6.1 percent of 244 bins inspected were infested.

T. glabrum populations were found in many of the bins of corn examined. In 1958, 7.8 percent of the 51 bins examined contained larvae or adults. In 1959, 19.6 percent of 224 bins were infested, and in 1960, *T. glabrum* was found in 7.7 percent of the 168 bins sampled.

Six hundred and thirty-five sorghum bins were sampled in 1960. Fifteen bins, or 2.4 percent, were infested. This low incidence of infestation may have occurred because the sorghum had been in storage for less than one year.

All larvae and adults collected from these samples were submitted to Dr. W. H. Anderson of the Insect Identification and Parasite Introduction Research Branch, U.S.D.A., for positive identification.

During the three-year survey period, infestations of *T. glabrum* were encountered in 41 counties in Nebraska. Two additional counties were found infested later when *T. glabrum* larvae and adults were collected in Harlan County in 1961 and Kimball County in 1962.

Grain bins in 21 counties were never sampled, as grain storages under Commodity Credit seal were non-existent at the time this survey was conducted. Counties where *T. glabrum* have been collected and definitely identified as to species are shown in Figure 1. *T. glabrum* is well established in eastern Nebraska and its presence in Kimball, Dundy, and Dawes Counties in the western part of the state indicates its distribution is probably statewide.

Although many grain bins were infested, these infestations were relatively light. In all infested bins observed, only one or two live larvae or adults were found per 1000-gram sample of grain, and only a few seeds in each infested sample showed feeding injury. These results are similar to those of Strong *et al.* (1959) in California. On the other hand, very heavy populations of *T. glabrum* occurred in stored wheat and corn in Kansas during 1955 and 1956 (White and McGregor, 1957).

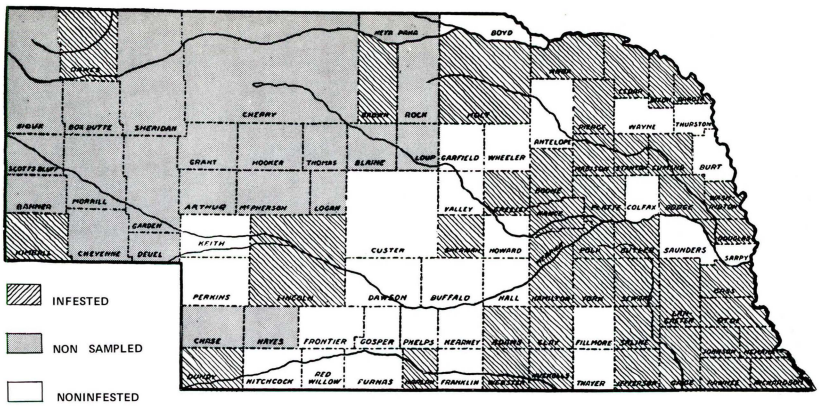

Figure 1. Known distribution of *Trogoderma glabrum* (Herbst) in Nebraska counties.

The light infestation of *T. glabrum* in Nebraska stored grain may stem from unfavorable environmental conditions. Laboratory studies show that heavy populations build up only when grain temperatures approach 90° F. Because stored grain in Nebraska reaches a temperature of 90° F. only for brief periods during the summer, population increase of *T. glabrum* is inhibited. Climatic conditions in California favor population increase, but the grain is stored for such a short time that the population has insufficient opportunity to increase. In Kansas, grain is stored for a long time and is subjected to extended periods of temperature exceeding 90° F.

BIOLOGICAL STUDIES WITH *Trogoderma Glabrum* (Herbst)

Stock Cultures

Stock cultures were maintained in one-gallon jars at 90° F. ± 2° and 65 to 70 percent relative humidity. Screens were glued over one-half inch holes in jar lids to provide air exchange. Two basic media were used. Medium A consisted of four parts finely ground cornmeal, four parts wheat shorts, two parts Purina dog food, one part honey, one-half part glycerol, one part rolled oats, and one-half part Brewers' yeast. These materials were mixed and added to an equal amount of whole hard red winter wheat adjusted to 15 percent moisture.

The second medium consisted of three parts whole and one part finely ground hard red winter wheat adjusted to 15 percent moisture. A tablespoon of Brewers' yeast was added to each quart of the mixture. Two quarts of either medium were placed in each jar with a folded paper towel standing upright to provide a surface on which the beetles could crawl. Fifty unsexed newly-emerged beetles were introduced into each culture.

The incidence of a disease caused by a schizogregarine protozoan was reduced to tolerable limits by autoclaving the culture jars and by surface sterilizing the beetles in a one percent sodium hypochlorite solution for one minute and rinsing them twice in clean water. The beetles were placed on a paper towel to remove excess moisture before being placed in the culture jars.

Cultures were discarded after one generation of *T. glabrum* to prevent an excessive increase of the protozoan population. Marzke and Dicke (1958) and Beal and Spitler (1959) found that the disease caused by this protozoan was very virulent in cultures of *T. glabrum* in the laboratory.

The Egg

Effect of Temperature on Egg Development

Eggs were collected in small plastic boxes (two and one-half inches long, one inch wide, and one inch deep), each containing one newly-emerged beetle of each sex. A small paper folded accordion fashion was placed in each box to prevent egg breakage by insect movement.

Beetles were transferred to new boxes each day to obtain eggs of known age. The eggs, laid on the bottom of the boxes and in the folds of the paper, were counted and observed *in situ* to avoid handling them. Four pairs of insects and the eggs produced by them were retained in constant environment cabinets set at 70°, 80°, 90° and 100° F. respectively, 65 to 70 percent relative humidity, and a daily photoperiod of 12 hours. Because beetles are inactive at 60° F., it was necessary to obtain eggs for this temperature from females held at 70° F.

As temperature increased, the length of the incubation period was reduced (Table 1). Although the hatch was reduced from 97.0 to 72.2 percent with an increase in temperature, the difference was not statistically significant. None of the eggs hatched at 60° F., but some showed partial development. At 70°, 80°, 90° and 100°, eggs which did not hatch showed no development.

The average incubation periods of *T. glabrum* eggs at all temperatures are comparable to those reported for *T. granarium* (Hinton,

Table 1. Average time required for development of *T. glabrum* eggs incubated at various temperatures with a relative humidity of 65 to 70 percent.

Temp. °F.	No. eggs	Avg. no. days to hatch	Range days	% Hatch[a]
60	125	0	0	0
70	101	11.5	11-13	97.0
80	115	7.7	7-10	85.1
90	77	5.9	5-6	80.1
100	90	4.3	4-5	72.2

[a] F-values are not significant.

1945; Lindgren *et al.*, 1955; Hadaway, 1956). At 70° F., the average incubation period of 11.5 days for *T. glabrum* eggs approximates the 14.0 days reported for *T. granarium* by Lindgren *et al.* (1955) and the 15.0 days reported by Voelkel (Hinton, 1945). At 80° F., the average incubation period of 7.7 days for *T. glabrum* eggs is comparable with the 8.0 days reported by Lindgren *et al.* (1955) and the 9 to 10 days shown by Hadaway (1956) at 77° F. for *T. granarium*. *T. glabrum* eggs required an average of 5.9 days at 90° F. which agrees with the 5.0 days for *T. granarium* obtained by Lindgren *et al.* (1955) and the 7.0 days determined by Voelkel (Hinton, 1945). Hadaway (1956) found that *T. granarium* eggs required an average of 4.5 days at 104° F. This is equivalent to the 4.3 days required by *T. glabrum* at 100° F. These two species have very similar temperature requirements for egg incubation.

The percentage hatch of *T. glabrum* eggs at 90° F. is comparable to the 75 percent hatch reported by Hadaway (1956) for *T. granarium* at the same temperature. Voelkel, however, obtained only 57.2 percent hatch for *T. granarium* at 90.5° F. (Hinton, 1945). The discrepancies between these results are perhaps explicable in the light of the results of Rahman *et al.* (1945). These authors obtained 41.5 to 86.8 percent hatch of *T. granarium* eggs depending upon the month of the year they were collected. The greatest hatch occurred in September.

The Larva

Feeding Habits of *Trogoderma glabrum* Larvae

Damage caused to stored wheat, corn, and sorghum by *T. glabrum* larvae is confined mainly to the germ portion of the kernels which is neatly eaten out. Feeding occurs on the endosperm and bran portion of the kernels only after the germ has been consumed. The endosperm may then be reduced to a finely ground flour.

T. glabrum does not penetrate deeply into masses of stored grain. Only the top two or three feet of grain are attacked and the grain surface may be very dusty from feeding waste, frass and cast skins. The accumulation of exuviae and metabolic waste products imparts a dead animal odor to the grain. This is very important in the grain trade as odor is used as one of the criteria for declaring grain unfit for human consumption.

At 90° F., the germs of 6 to 10 wheat kernels are consumed by a *T. glabrum* larva destined to become a male beetle whereas the germs of 9 to 15 kernels are necessary for development of a female beetle larva.[2] There are about 13,500 kernels in a pound of wheat; a bushel of wheat can then support over 80,000 *T. glabrum* larvae for the entire larval period.

[2] Hereafter, these will be referred to as female or male larvae.

Larval Instars

The number of larval instars and the lengths of the stadia for *T. glabrum* were determined by rearing larvae on a mixture of whole wheat flour and wheat germ adjusted to 15 percent moisture content. Larvae were retained in open salve tins one and one-half inches deep which were placed in dessicator jars kept at 90° F. and a daily photoperiod of 12 hours.

Results obtained under these optimum conditions are shown in Table 2. With the exception of three larvae which molted six days after emerging from the egg and which eventually developed into females, all larvae underwent their first molt five days after hatching. Six of the larvae which developed into females molted five times; the other four molted six times. Two larvae which later developed into males molted four times; the others molted five times.

These results agree closely with those reported for *T. granarium* by Hadaway (1956) at 95° F. *T. granarium* larvae which developed into males required four or five molts compared with five molts required for larvae which developed into females. Hadaway (1956) concluded that *T. granarium* female larvae usually require one more molt than do male larvae.

With these optimum conditions, 24 of the original 28 larvae pupated. Each larva molted by splitting the integument along the middorsal ecdysial line to the fifth or sixth abdominal segment and crawling out of this split. The newly-molted larva resumed feeding immediately.

Observations on larval development under adverse conditions created by low temperature, starvation, or high disease incidence showed that *T. glabrum* larvae molted 11 or 12 times. Hadaway (1956) mentions that *T. granarium* larvae molted as many as eight times at lower temperatures.

Effect of Higher Temperatures and Rearing Media on Larval Development and Survival

Larvae were reared in constant environment cabinets at 70°, 80°, 90°, and 100° F. and 65 to 70 percent relative humidity in five-dram glass vials containing five grams of either Medium A or whole wheat flour, ground from Pawnee hard red winter wheat and adjusted to 15 percent moisture content. Moisture determinations were made with a Brown-Duval tester or by the two stage oven method. A single newly-hatched larva was placed in each vial.

The average lengths of the larval period for *T. glabrum* on both media are shown in Table 3. As the temperature increased, the larval period on Medium A became shorter and the number of larvae surviving to the pupal stage increased. Although the average number of

Table 2. The average number of days for each stadium and for larval development of *T. glabrum* at 90° F. when reared on whole wheat germ and flour.

Sex of emerged adult	No. larvae observed	Avg. no. days of stadia						Avg. no. days from last molt to pupa	Avg. no. days as larva
		1st	2nd	3rd	4th	5th	6th		
Female	10	5.3	4.3	4.7	4.7	5.3	6.0	7.7	34.7
Male	14	5.0	4.4	4.9	4.9	5.9		6.5	29.8

Table 3. Average number of days required for *T. glabrum* larval development and percent larval survival at various temperatures and a relative humidity of 65 to 70 percent on either Medium A or whole wheat flour adjusted to 15 percent moisture.

Temp. °F.	*Medium A*			*Whole Wheat Flour*		
	No. larvae	Avg. no. days to pupa[1]	% Survival	No. larvae	Avg. no. days to pupa[1]	% Survival
70	94	139.0 a	41.5	50	120.4 a	10
80	200	38.7 b	66.5	50	36.2 b	52
90	200	25.5 c	84.7	50	30.7 b	48
100				50	35.4 b	60

[1] All means followed by the same letter are not significantly different according to Duncan's multiple range test at the 1 percent level.

days required for completion of larval development on Medium A compared favorably with those on whole wheat flour, larval survival at all temperatures was markedly greater on Medium A than on whole wheat flour.

The composition of the medium had no appreciable affect on the length of the larval developmental period but did influence the capacity of the larvae to survive. It is conceivable, however, that the composition of the medium may also alter the time required for larval development. The results obtained by Lindgren *et al.* (1955) and by Voelkel (Hinton, 1945) with *T. granarium* are indicative of this. Lindgren *et al.* determined the average number of days for larval development of the Khapra beetle to be 190 at 70° F., and 148 at 80° F. Voelkel's average time periods were 47 days at 70° F. and 40 days at 80° F. The only difference in the experimental procedures employed by Lindgren *et al.* and Voelkel was in the larval rearing media; Lindgren *et al.* used dog food whereas Voelkel used barley malt. This diversity of diet appears to be a logical explanation for the disparity in results.

It appears from Table 3 that a temperature of about 90° F. favors larval development and survival of *T. glabrum*. This is true for either male larvae or female larvae developing on Medium A (Table 4). At all temperatures the female larvae required a significantly longer time to complete their development than did the male larvae. The average male larval period was 14.1 days less than the average female period at 70° F., 5.9 days less at 80° F. and 2.8 days less at 90° F. These results are similar to those of Hinton (1945), Hadaway (1956) and Lindgren *et al.* for *T. granarium*.

When male and female larvae were reared on whole wheat flour, larval survival was materially reduced. The small number of larvae surviving at 70° F. obviated any conclusion on the effect of this temperature on the developmental periods of male and female larvae.

At 80° F. the average time required for the development of male larvae, 34.4 days, was significantly shorter than that required for female larvae, 38.6 days ($t_{0.05} = 2.373$ with 24 df). The average de-

Table 4. Average number of days required for male and female larval development on Medium A at various temperatures and a relative humidity of 65 to 70 percent.

Temp. °F.	No. observations		Avg. no. days to pupa	
	Males	Females	Males	Females
70	19	20**	131.8	145.9
80	66	67**	35.7	41.6
90	85	74*	24.2	27.0

** Significant at 1 percent level by the t-test.
* Significant at 5 percent level by the t-test.

velopmental times for larvae ultimately becoming males and females were 29.8 and 32.7 days, respectively, at 90° F., and 34.2 and 36.6 days, respectively, at 100° F. These differences, however, were not statistically significant owing to the limited number of observations resulting from the demise of so many larvae on whole wheat flour. In spite of this dietary effect, the female developmental periods were longer than those of the males, and the optimum temperature for development of larvae of both sexes was again about 90° F.

Rahman *et al.* (1945) determined the male and female larval periods of *T. granarium* when the larvae were provided ground wheat at a temperature of 86° F. Their results, 26.0 days for larvae developing into males versus 35.2 days for female larvae, are quite comparable to the results obtained with *T. glabrum* under similar conditions. Apparently the developmental periods of male and female larvae of *T. glabrum* and *T. granarium* are similar.

Larval Development on Whole Wheat Kernels

Some species of stored grain insects such as the saw-toothed grain beetle, *Oryzaephilus surinamensis* (L.), and the confused flour beetle, *Tribolium confusum* Duval, cannot feed on whole grain. These insects can survive only on cracked and pitted kernels. An experiment was conducted to determine whether the larvae of *T. glabrum* can attack whole grain.

Wheat adjusted to 15 percent moisture was placed in five-dram vials. These were placed in a desiccator jar over a super-saturated sodium chloride solution which maintained a relative humidity of 75.5 percent at 90° F. (Winston and Bates, 1960). Wheat in equilibrium with a relative humidity of 75 percent at 90° F. contains about 15 percent moisture. Sound kernels of Pawnee wheat were selected by examination under a dissecting microscope. One newly-hatched larva was placed in each of 20 vials with 30 sound wheat kernels per vial and in each of 20 vials containing one gram of whole wheat flour milled from Pawnee wheat.

Larval development was delayed significantly when the larvae were reared on whole wheat (Table 5). This delay was not reflected in larval survival; about the same number of larvae survived on both whole wheat and whole wheat flour. First instar larvae of *T. glabrum* definitely can attack and exist on wheat with the seed integument intact.

The increase in the time necessary for larval development on whole wheat was not associated with the ultimate sex of the larvae. On whole wheat the average time of development of either male or female larvae was significantly longer than that of corresponding larvae reared on whole wheat flour. On both diets, the female larvae required a significantly longer time to pupate than did the male larvae. The aver-

Table 5. Average number of days required to pupation of *T. glabrum* larvae on whole wheat kernels and whole wheat flour at 15 percent moisture with a temperature of 90° F. and 75 percent relative humidity.

Medium	Avg. no. days to pupation all larvae	Avg. no. days to pupation		% Survival
		Males	Females	
Whole wheat kernels	36.2*	33.5	38.5*	50
Whole wheat flour	32.0	30.4	33.6**	65 ns

* Significant at the 5 percent level.
** Significant at the 1 percent level.
ns Not significant.

age time to pupation on whole wheat flour in this experiment compared favorably with results from previous experiments in which larvae were reared on this medium at the same temperature (Table 3).

According to Hinton (1945), *T. granarium* is unable to attack sound wheat kernels. Hadaway (1956) to the contrary found that *T. granarium* larvae could attack whole kernels by biting through the weaker part of the bran. Hadaway's results are similar to those presented here for *T. glabrum*. The moisture content and variety of the whole grain may influence the ability of *T. glabrum* and *T. granarium* to feed on it. Sound kernels with a moisture content of 15 percent are suitable for development of first instar larvae of *T. glabrum*.

The Influence of Cracked Grain and Grain Moisture Content on Larval Development and Survival

The time necessary for larval development and the rate of larval survival should be a function of the type of grain, the number of larvae per unit grain mass, the amount of cracked grain, and, perhaps, the grain moisture content.

It has already been established that larvae of *T. glabrum*, on the average, consume the germs of 10 wheat kernels to complete their development. There are approximately 2,100 kernels in 100 grams of wheat. If it is assumed that the larvae seek out and feed only on cracked kernels when offered a choice between whole wheat and damaged kernels, and if one percent of the kernels in 100 grams of wheat are cracked, only two of 20 larvae should survive.

If a greater number of larvae should survive under these conditions, then some of the larvae must feed on whole grain and the time necessary for larval development should be increased. If 10 percent of the 100 grams of wheat is cracked, all 20 of the larvae should be able

to complete their development on cracked grain, the larval survival rate should increase, and the time of larval development should be reduced. With a greater amount of cracked wheat, there should be no further increase in the larval survival rate or an appreciable decrease in the larval developmental period.

An experiment was designed using Pawnee hard red winter wheat with a moisture content of either 12 or 15 percent to determine whether these assumptions and relationships were correct.

The diets containing 1, 10 and 50 percent cracked kernels were prepared by adding the required amounts of damaged kernels to whole grain. The damaged grain was produced by coarse grinding through a grinding machine. After the grain moisture content was stabilized, 100 grams of each diet were placed in each of 10 half-pint jars and 20 newly-emerged first instar larvae were added to each jar.

A five-dram vial with a one and one-half-inch cotton wick soaked in a five percent solution of potassium hydroxide was placed in each jar. A screen was placed over the vial to allow the absorption of carbon dioxide from the jar by the potassium hydroxide. The tightly sealed jars were opened daily to record the number of larvae pupating.

Grain moisture determinations made at the completion of the experiment showed that the moisture levels remained constant throughout the experiment. Results of this experiment are presented in Table 6.

At both moisture levels, the time for larval development was significantly increased and the rate of survival was reduced when the larvae were offered wheat with one percent damaged kernels. This detrimental effect was mitigated when the larvae were fed 10 percent cracked wheat; no further mitigation occurred when the larvae were fed 50 percent cracked wheat.

The survival rates on one percent cracked wheat were sufficiently high to indicate that larvae of *T. glabrum* will feed upon whole wheat in the absence of damaged wheat, but this reduces the size of the insect population. The data obtained on 10 percent cracked wheat, essentially the same as those on 50 percent cracked wheat, infer that the larvae seek out and feed upon cracked grain. Also, the amount of cracked grain in a mass of wheat, relevant to the number of larvae attempting to feed on that mass, determines to a high degree the extent of the insect population. It appears that the moisture content of wheat within the limits usually encountered in storage does not influence these relationships.

A similar experiment was conducted in which 501D yellow-dent hybrid field corn was employed. Results of this experiment (Table 7) show that the relationships established for wheat apparently do not entirely apply when *T. glabrum* feeds on corn. Obviously, the amount of cracked corn is important in determining the size of the insect

Table 6. Average time of larval development and percent survival at 90° F. on cracked wheat with a moisture content of either 12 or 15 percent.

% Grain moisture	% Damaged kernels	Avg. no. days to pupation—male larvae	Avg. no. days to pupation—female larvae	Avg. no. days to pupation—both sexes[1]	No. males	No. females	% Survival to pupation—both sexes[1]
15.0	1	30.3	33.9	31.7[a]	58	45	51.5[a]
	10	26.2	33.5	29.8[b]	82	76	79.0[b]
	50	25.9	31.7	28.8[b]	97	75	86.0[b]
12.0	1	33.1	42.2	36.9[a]	39	37	62.9[a]
	10	28.1	36.4	31.6[b]	91	63	77.0[b]
	50	27.4	30.9	29.1[b]	82	78	80.0[b]

[1] All means followed by the same letter are not significantly different according to Duncan's multiple range test at the 1 percent level. Separate statistical analysis was applied to the data obtained at each grain moisture level.

Table 7. Average time of larval development and percent survival at 90° F. on cracked 501D yellow-dent hybrid field corn with a moisture content of either 12 or 15 percent.

% Grain moisture	% Damaged kernels	Avg. no. days to pupation—male larvae	Avg. no. days to pupation—female larvae	Avg. no. days to pupation—both sexes[1]	No. males	No. females	% Survival to pupation—both sexes[1]
15.0	1	41.2	45.5	41.3[a]	34	28	31.0[a]
	10	30.7	34.8	32.7[a]	84	93	88.5[b]
	50	35.5	36.1	33.7[a]	64	69	66.5[c]
12.0	1			48.3[a]	3	0	1.5[a]
	10	28.7	34.3	29.3[b]	55	14	34.5[b]
	50	31.5	35.0	32.4[c]	46	26	36.0[c]

[1] All means followed by the same letter are not significantly different according to Duncan's multiple range test at the 1 percent level. Separate statistical treatment was applied to the data obtained at each grain moisture level.

population, for at both moisture levels the larval developmental periods were significantly increased and the survival rates were reduced on one percent cracked corn. But the moisture content of the corn also seems to influence the growth and survival of *T. glabrum* larvae. This is seen in the high survival rate on 10 percent cracked corn with a 15 percent moisture content, the low survival rates on all three diets with a 12 percent moisture content, and the lengthened developmental period on 50 percent cracked corn at the lower moisture level.

The disproportionately greater number of male beetles which arose from larvae maintained on corn with a moisture content of 12 percent may have reflected the relative incapacity of female larvae to survive on diets detrimental to larval growth. With a limitation of food necessary for proper development, the greater food requirements of the larger female larvae would place them in jeopardy. The smaller male larvae, requiring less food, would have more of a chance to survive. Hinton (1945) reports that various authors have observed this predominance of larvae developing into male adults of *T. granarium* under adverse conditions such as low temperatures and poor quality food. With both *T. glabrum* and *T. granarium*, the adult sex ratio is apparently influenced by the nature of the larval food and other environmental factors affecting the larvae.

Under all conditions in both experiments, female larvae required more time to complete their development than did male larvae.

The capacity of *T. glabrum* larvae to survive on Martin sorghum with one percent cracked kernels and a moisture content of 15 percent was investigated in the manner already described for wheat and corn. The larval survival rate was 34.5 percent, a rate equivalent to that on one percent cracked corn at the same moisture level. Female larvae required an average of 36.5 days to complete their development; male larvae required 30.1 days. *T. glabrum* appears quite capable of maintaining itself in stored sorghum.

Effect of Low Temperature on Larval Survival

A limited investigation was made on the ability of *T. glabrum* larvae to survive at reduced temperatures. Mortality rates of one- to three-day-old larvae, held individually in vials containing whole wheat flour, were determined after exposure periods of 13, 20, 30, 40 and 50 days at a temperature of 36° F. and after 110 and 150 days at a temperature of 60° F.

For each exposure period, 10 larvae were removed from the constant environment cabinet and retained at 90° F. for several days before mortality was noted. When larvae were subjected to a temperature of 36° F., they all survived for 13 days. Forty percent had died after 20 days, 60 percent after 30 days, 80 percent after 40 days, and all

were dead after 50 days. At 60° F., 90 percent of the larvae survived for 110 days and 30 percent were alive after 150 days. Exposure to reduced temperatures, although deadly if maintained long enough, did not cause harmful physiological effects once the larvae were restored to a favorable temperature. All surviving larvae matured and pupated normally.

Although the temperature of grain in storage may dip to 36° F. in Nebraska, there are invariably areas within the grain mass that are considerably warmer. Living larvae of *T. glabrum* were found in numerous grain bins in late fall and early winter. Larvae were collected in one grain storage in late March after having successfully passed the winter; at this time the grain temperature was 50° to 60° F. while the outside temperature was substantially lower.

Effect of Starvation on Larval Survival

Although no detailed studies were made on the effect of starvation on *T. glabrum* larvae, observations showed that larvae of this species can remain active for long periods without food. Ten two-week-old larvae survived two months at 80° F. According to Beal (1954), *T. granarium* and *T. versicolor* larvae can endure periods of starvation of two to five years. Thus, this ability to live for long periods without food appears to be a characteristic of all *Trogoderma* larvae. This enables these species to persist in empty storages for long periods and to reinfest grain when the bins are filled.

Effect of Disease on *Trogoderma glabrum* Larvae

Three serious disease outbreaks in the *T. glabrum* cultures over a three-year period made it necessary to discard numerous experiments. Samples of infected larvae were collected twice and submitted to Dr. Edward A. Steinhaus of the Insect Pathology Laboratory, University of California, who identified the pathogen as a protozoan belonging to the *Mattesia* group.

Cultures were most obviously and apparently most rapidly infected at 80° F. After the first diseased larvae were observed, the whole culture was infected within two months at this temperature. Severely infected larvae failed to pupate, gradually shrinking in size with a flattening of the abdomen. Many individuals at all temperatures were observed to die in the pupal stage. These pupae contained numerous spores of the schizogregarine parasite. Marzke and Dicke (1958) showed that the parasite is transmitted from larva to larva of *T. inclusum* and that five other *Trogoderma* species could be infected to various degrees. Beal and Spitler (1959) reported that *T. granarium* appeared tolerant to this disease, whereas *T. glabrum* was completely susceptible.

Field collections of *T. glabrum* larvae, made at two locations in Nebraska, were found to contain infected larvae. White and McGregor (1957) collected diseased specimens from several locations in Kansas, and Marzke and Dicke (1958) encountered the disease in laboratory cultures of *T. glabrum*. It appears that the disease is well established in nature and may exert some influence on population development in the field.

The Pupa

Effect of Higher Temperatures on Pupal Development and Survival

Pupal development and survival were determined in constant environment cabinets at 70°, 80°, 90°, and 100° F. and 65 to 70 percent relative humidity. The pupae, retained in five-dram vials, were observed daily from the time of pupation to adult emergence. Although female pupae are larger than male pupae, all sex determinations were based on the emerging adults.

The best temperature for pupal development was 100° F. (Table 8). The high rate of survival at all temperatures may perhaps be related to the manner in which *T. glabrum* pupates. The pupal period is passed in the last larval skin, a trait characteristic of all species of *Trogerderma* (Beal, 1954). The larval skin may provide the pupa with a protective covering; when occasionally a pupa became dislodged from its covering, it soon died.

Effect of Low Temperature on Pupal Survival

Three-day-old pupae in five-dram vials were exposed to a temperature of 36° F. and 65 to 70 percent relative humidity in a constant environment cabinet. Ten pupae were removed after one, six, and 12 days and were held at 90° F. for adult emergence; 10 pupae were retained constantly at 90° F.

Exposure to this relatively low temperature for approximately two weeks was fatal for all pupae. The rates of survival were 70 percent and 60 percent respectively for those pupae exposed one day and six

Table 8. Average number of days required for development of *T. glabrum* pupae at 70°, 80°, 90° and 100° F. and a relative humidity of 65 to 70 percent.

Temp. °F.	No. pupae	Avg. no. days		No. emerged adults		% Survival
		Male pupae	Female pupae	Male	Female	
70	34	7.1	9.1	17	16	97
80	61	6.0	5.6	25	36	100
90	118	4.8	4.0	64	52	98
100	40	3.3	3.3	19	20	97

Table 9. Average number of days that newly-emerged *T. glabrum* adults spent in last larval skins at various temperatures and a relative humidity of 65 to 70 percent.

Temp. °F.	No. adults	Avg. no. days		% Survival
		Males	Females	
70	33	7.5	6.4	100
80	61	4.6	3.6	100
90	116	2.8	3.2	100
100	39	2.2	1.3	100

days whereas 90 percent of the unexposed pupae survived. If the last larval skin does indeed protect the pupae, it is insufficient at low temperatures. Lindgren *et al.* (1955) found that pupae of *T. granarium* were very susceptible to freezing temperatures when exposed for short periods of time.

Quiescent Period of Newly-Emerged Adults

On completion of the pupal period, the adult forces the pupal exuvium into a wad at the posterior end of the last larval skin but remains for a time within the last larval skin. When newly-emerged adults were subjected to temperatures of 70°, 80°, 90°, and 100° F., the time spent in the quiescent state was reduced as the temperature increased (Table 9).

The Adult

Newly-emerged males and females were paired in small plastic boxes containing strips of paper, folded accordion fashion, to provide an oviposition surface. Only unmated adults which had emerged at about the same time were used. Sex determinations were made on the basis of body size and antennal characteristics (Beal, 1954).

Several pairs of beetles were placed in constant environment cabinets set at 70°, 80°, 90°, and 100° F. and a relative humidity of 65 to 75 percent. Daily observations were made to determine mating habits, the effect of temperature on the duration of the preoviposition and oviposition periods and on egg production, the feeding habits of gravid females, the egg laying pattern and the production of unfertilized eggs, and the effect of temperature on adult longevity.

Mating Habits

Mating occurred immediately after the adults left the last larval skin. Mating behavior was observed twice under the dissecting microscope. Preceding copulation, the males appeared to be stimulated to sexual activity when their mouth parts or antennae contacted the

dorsal setae of the females. Copulation was completed in 55 and 70 seconds during the daylight hours but under artificial light. Hinton (1945) reported that *T. granarium* usually mates during the night.

Effect of Temperature on the Duration of the Preoviposition and Oviposition Periods and on Egg Production

The preoviposition period was found to vary with temperature. This period was two to three days at 70°, one to two days at 80°, and one day at 90° and 100° F. The duration of the egg laying period also was found to vary with temperature. At 90° and 100° most eggs were produced during the first two days, at 80° most eggs were laid in the first four days, and at 70° F. eggs were laid over a period of a week.

Peak egg production occurred at 80° F.; egg laying was reduced at 70° and 90° and greatly reduced at 100° F. (Table 10). Hadaway (1956) found that the average number of eggs laid by *T. granarium* was 30 to 50 at 86° F. Evidentally *T. glabrum* is more prolific than *T. granarium.*

Feeding Habits of Adults, Egg Laying Pattern, Production of Unfertilized Eggs

Neither sex was observed to feed, but this fasting habit in no way influenced oviposition. In numerous dissections, invariably the gut was empty several days after the female had emerged from the puparium. Hinton (1945) stated that females of *T. granarium* do not feed either.

Eggs were usually laid singly and randomly in whole wheat. No definite pattern of egg placement was seen. Rahman *et al.* (1945) found that the eggs of *T. granarium* also are usually scattered among the grain.

Although commonly *T. glabrum* females laid fertilized eggs, unfertilized eggs were produced. One virgin female laid five eggs whereas three others together produced 14 eggs. No apparent embryonic development took place in those eggs.

Table 10. Average number of eggs oviposited by *T. glabrum* females at four temperatures with a relative humidity of 65 to 70 percent.

No. females	Temp. °F.	Avg. no. eggs/female[1]
5	70	63.6[a]
10	80	92.0[b]
11	90	68.0[a]
5	100	36.6[c]

[1] All means followed by the same letter are not significantly different by Duncan's multiple range test at the 5 percent level.

Table 11. Longevity of *T. glabrum* adults at four temperatures with a relative humidity of 60 to 70 percent.

Temp. °F.	No. observations	Sex	Condition maintained	Longevity range (days)	Avg. longevity (days)
70	10	F	mated	21-37	25.9
	19	F	unmated	29-50	42.0
	10	M	mated	11-28	23.7
80	10	F	mated	8-13	10.5
	12	F	unmated	21-32	26.0
	10	M	mated	9-15	10.8
	10	M	unmated	18-35	28.5
90	11	F	mated	5-11	8.7
	10	F	unmated	8-20	15.9
	11	M	mated	5-12	8.7
	13	M	unmated	10-18	14.2
100	5	F	mated	3-9	7.2
	6	F	unmated	8-29	15.9
	6	M	mated	3-8	5.1
	5	M	unmated	4-8	6.6

Effect of Temperature on Adult Longevity

Longevity of both males and females decreased with an increase in temperature, but unmated males and females survived longer than their mated counterparts (Table 11). The unmated males were less active and may have conserved energy through decreased sperm production. It was noticed that gravid females became smaller as the eggs were laid with the body wall often collapsing completely a few days before death. The average life spans of mated males and females were essentially the same.

INTERNAL TRANSMISSION OF STORED-GRAIN FUNGI BY LARVAE, PUPAE AND ADULTS OF *TROGODERMA GLABRUM*

The bristly larvae and adults of *T. glabrum* can easily transport spores of stored grain fungi on their bodies throughout the grain mass. Early instar larvae in very moldy grain become so laden with fungus spores that some are unable to move. *T. glabrum* may be an efficient vector of fungus pathogens of grain by ingesting spores, transporting them internally, and voiding them in a viable state in the feces. Experiments were conducted to determine whether spores of several species of *Aspergillus* might survive passage through larvae, pupae, and adults of *T. glabrum*.

Methods and Materials

The larval media were usually infected with nine species of *Aspergillus: A. repens, A. chevalieri, A. ruber, A. restrictus, A. amstelodami, A. flavus, A. candidus, A. ochraceus,* and *A. niger.* The standard medium used in all fungus isolations consisted of one to two percent agar-agar, two percent malt extract, and 10 percent sodium chloride (Christensen, 1957). Christensen (1957) stated that this medium best served to isolate the largest number of fungi associated with stored grain deterioration.

Surface sterilization of the various stages of the insect was accomplished with a slight modification of the procedure described by Agrawal *et al.* (1957).

To determine whether *Aspergillus* spores ingested by larvae are viable in the feces, twenty 30-day-old larvae, taken from whole wheat heavily infected with *Aspergillus,* were surface sterilized, placed individually in sterile petri dishes, and removed after 24 hours when the fecal pellets were counted and marked, and a thin layer of the standard medium poured into the dishes. To find out how long larvae excrete fungus-contaminated feces, 10 surface-sterilized larvae, held singly in one-inch sections of sterile glass tubing so that they were unable to turn around, were fed sterile food in one end of the tube while their fecal pellets were collected daily from the other.

One hundred pupae within and 10 pupae without the last larval exuviae were surface sterilized and plated out whole on the standard medium. Ten pupae without and 60 pupae within the last larval exuviae were obtained from larvae reared on wheat heavily infected with *Aspergillus.* Forty pupae retained in the last larval exuviae arose from larvae reared on lightly infected wheat. The larval rearing media were prepared by adding wheat infected with eight species of *Aspergillus* to non-infected wheat and whole wheat germ so that the heavily infected medium contained 5,200,000 and the lightly infected medium contained 700 viable spores per gram as determined by the viable-spore-count method of Christensen (1957).

Feces of adults reared on wheat heavily infected with *Aspergillus* were collected and cultured by surface sterilizing 20 newly-emerged beetles, placing them for 48 hours in petri dishes containing the standard medium, after which their fecal pellets were marked and observed for fungal growth. To determine whether beetles would feed on fungus spores and mycelium, 35 beetles, offered these materials for seven days, were dissected and their intestinal tracts examined. An equal number of beetles were offered bee pollen, a substance on which they would reasonably be expected to feed.

The capacity of surface-sterilized larvae and adults to infect sterile wheat by spore-contaminated feces was determined by placing individual larvae or adults in vials containing 10 grams of sterile wheat ad-

justed to a 18 percent moisture content. The sterile wheat was obtained by autoclaving at 15 psi for two hours followed 24 hours later by further autoclaving for one hour. Twenty 35-day-old larvae and 10 two-day-old adults, reared on media containing either 5,200,000 or 700 viable spores per gram, were tested.

The effect of moldy wheat on larval development was ascertained by placing 100 newly-hatched larvae individually in vials containing 30 wheat kernels heavily infected with *Aspergillus* and examining the larvae daily through the second molt.

The pure cultures of the fungus species were isolated and identified as to species by procedures described by Thom and Raper (1945). Species determinations were confirmed by Dr. W. W. Ray, then Chairman of the Botany Department at the University of Nebraska, and Dr. C. M. Christensen, Professor of Plant Pathology and Botany, University of Minnesota.

Results

Seventy-three percent of the fecal pellets voided by 16 larvae contained viable spores of *A. repens, A. chevalieri, A. ruber, A. restrictus, A. amstelodami, A. flavus* and *A. candidus.* Although the larvae possibly ingested spores of *A. niger* and *A. ochraceus,* these two species were not present in the feces. *A. repens* and *A. chevalieri* occurred most commonly. Four larvae passed 29 uncontaminated fecal pellets.

Nine of the 10 larvae confined in the glass tubing voided contaminated feces after 24 hours, two after 48 hours, and none after 72 or 96 hours. The larvae must continually ingest *Aspergillus* spores to void contaminated feces constantly.

All *Aspergillus* species isolated from the feces of larvae, and including *A. niger,* were found in surface-sterilized pupae. All the pupae derived from larvae reared on heavily infected wheat, including the 10 pupae removed from the last larval exuviae, contained viable spores of several species of *Aspergillus.* Only 10 of the 40 pupae from larvae reared on lightly infected wheat harbored spores. The number of pupae bearing fungi internally was obviously influenced by the degree of fungal infection in the larval media. Because larvae do not retain spores internally for more than 48 hours, the pupae must become contaminated with spores ingested by the larvae immediately before pupation. Fungi borne internally in pupae would be of no importance in initiating new infections in stored grain unless the pupae were accidentally crushed by moving grain.

Fifteen adults passed feces with viable *Aspergillus* spores during the first two days after emergence, but no contaminated feces was found thereafter. The fungi isolated were *A. repens, A. restrictus, A. flavus,* and *A. ruber.* After four days the beetles egested a watery fluid containing little solid material. Because these beetles were not pro-

vided with food, their internal fungi must have been obtained through the pupae. Fungus spores were evidently discharged with pupation wastes soon after adult emergence.

No bee pollen, fungus mycelium or spores could be found in the dissected digestive tracts of beetles offered these materials. This is further evidence that adults of *T. glabrum* do not feed and that internal fungi must pass through the pupae.

Eighteen larvae and nine adults, reared on heavily infected wheat, transmitted fungi to sterile wheat through their feces whereas nine larvae and four adults reared on lightly infected wheat did so. These significant differences show that the efficiency of larvae or adults in transporting internally species of *Aspergillus* throughout the grain mass is influenced by the degree of fungal infection in the insect-infested grain.

Newly-hatched larvae, exposed to very moldy wheat, picked up so many spores and bits of mycelium on their legs that some were unable to move. The population of *T. glabrum* can be somewhat reduced in very moldy grain through the death of encumbered first instar larvae. Older larvae were unimpeded because they were able to shake off the fungal material. No evidence was obtained that moldy grain can poison larvae of *T. glabrum*.

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