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Postharvest Biology and Technology 7 (1996) 371–380

Postharvest Biology and Technology

Heat production by adult *Cryptolestes ferrugineus* (Stephens) of different ages and densities

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Accepted 15 August 1995

Abstract

The heat of respiration of adult *Cryptolestes ferrugineus* at three ages (one, four, and eight weeks old) at 2500 insects/200 g of wheat and three population densities (1250, 2500, and 5000 insects/200 g of wheat) with four-week old insects was measured in a computer-controlled, adiabatic respiratory calorimeter at three initial grain temperatures (15, 25, and 35°C) and three moisture contents (MCs) [12, 15, and 18% wet basis (WB)]. Age, density, temperature, and MC significantly affected heat production ($P < 0.001$). Heat production rates increased with both increasing initial grain temperature and moisture content. Heat production by age was highest in four-week old adults (9.41 μW/insect), whereas that of eight-week old adults (7.81 μW/insect) was slightly higher than for adults one week old (7.40 μW/insect). Heat production per insect by density was highest at 2500 insects/200 g of wheat (9.41 μW/insect) and lowest at 5000 insects/200 g of wheat (6.38 μW/insect). Instantaneous rates of heat production measured over the test period were affected by the combination of age, density, moisture content, and temperature increase.

Keywords: Heat production; Age; Density; Temperature; Moisture content; *Cryptolestes ferrugineus*

1. Introduction

Metabolic heat production by insects has been suspected to be the main cause of hot spots and heating in dry grain (Back and Cotton, 1924; Oxley, 1948). Howe (1962) described insect-induced hot spots as the result of insect metabolic heat accumulating to produce a small local rise in temperature, which accelerates both the metabolism of insects and their rates of multiplication, and thus, continuously

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SSDI 0925-5214(95)00050-X

increasing the amount of metabolic heat produced. He also observed that the amount of heat produced by an insect population depends on the density of the population and the conditions of the microenvironment, especially the temperature and moisture content (MC) of the surrounding grains. *Cryptolestes ferrugineus* (Stephens) (Coleoptera: Cucujidae) is a major pest of stored grain in Western Canada where it is associated with grain heating and hot spots in field granaries (Sinha and Wallace, 1965, 1966).

Insect heat production in stored wheat under adiabatic conditions was significantly affected by initial grain temperature, grain moisture content, and grain mechanical condition (Cofie-Agblor 1994). As part of a programme to simulate insect heat production and hot spot development in granaries using laboratory data of insect heat production under various storage conditions, the research reported in this paper set out to determine the effects of adult age and population density on the heat production of *C. ferrugineus* at different initial grain temperatures and moisture contents under adiabatic conditions.

2. Materials and methods

Equipment and materials

Heat production was measured by the temperature rise of 200 g of wheat and insects in an adiabatic-calorimeter flask. The respiratory calorimeter, and the determination of the heat capacities of the calorimeter flasks and the specific heat of wheat were described by Cofie-Agblor (1994) and Cofie-Agblor et al. (1995). The wheat used for insect rearing and the tests was hard red spring wheat (cv. Katepwa, registered seed, United Grain Growers, Winnipeg, Man.). Particle density of the wheat was determined by measuring the volume of a known mass of grain using the air comparison pycnometer (Beckman Instruments, Inc., Fullerton, Calif.) and the results were confirmed by the method of specific gravity bottle using toluene. Kernels were broken by passing the wheat through a plate mill and then sieving out the fines and smaller fragments with a sieve of 1.168-mm aperture.

The insects were reared on coarsely-ground and broken wheat of approximately 14% moisture content, wet basis (WB) at 30 ± 1°C and 70 ± 5% relative humidity (RH).

Experimental procedure, design, and analyses of data

The experiments were conducted as described by Cofie-Agblor (1994) and Cofie-Agblor et al. (1995) on 200-g samples of wheat with 20% broken kernels. Completely randomized, factorial experiments were designed to measure the effect of insect age and population density on the heat production of adult *C. ferrugineus* at different initial grain temperatures and moisture contents. In Experiment I, the heat production of three ages (one, four, and eight weeks old) was measured at three initial grain temperatures (15, 25, and 35°C) and three moisture contents (12, 15, and 18% WB). The insect population density was 2500 insects/200 g sample of wheat. Experiment II measured the heat production of four-week old adult insects at three densities (1250, 2500, and 5000 insects/sample of wheat) at the same conditions of initial grain temperature and moisture content stated for adults of different ages. The selection of insect densities was based on exploratory tests that determined densities at which measurable temperature rise and CO_2 were produced within 24 h of the test. Each condition in each experiment had four replicates and the measurements lasted 20 h at 15° and 25°C, and 12 h at 35°C. The test duration was also determined from exploratory experiments that determined the effect of cumulative CO_2 of respiration on insect respiration. Experiment I with four-week old adults provided the second density level (2500 insects/sample of wheat) for Experiment II. The experimental data were analyzed as described by Cofie-Agblor et al. (1995) and analysis of variance was performed on each experiment using the General Linear Model Procedure (GLM) from PC SAS (SAS Institute Inc., Cary, N.C.).

3. Results

Effect of experimental variables on heat production

Analysis of variance for both experiments showed that the variables and their interactions significantly affected heat production ($P < 0.001$). Of the four variables tested, temperature influenced heat production the most, moisture content caused moderate changes, whereas age and density had significant but minor effects. In Experiment I, heat production increased with increasing temperature from 15 to 35°C (Fig. 1a). The factor of increase in the rate of heat production for a 10°C rise in temperature, or Q_{10}, was 3.0 from 15 to 25°C and 2.7 from 25 to 35°C. Heat production also increased with increasing moisture content (Fig. 1b). The mean heat production rate at each temperature and moisture content were significantly different ($P = 0.05$, using the Duncan's new multiple range test, DMRT). Heat production by age was greatest with four-week old adults with an average of 9.41 μW/insect, which was 20% more than that produced at eight weeks of age. One-week old adults produced the least heat, averaging 7.40 μW/insect (Fig. 1c). The mean heat production rates for age were significantly different at $P = 0.05$ (DMRT).

The main effect of temperature and moisture content in Experiment II was similar to that of Experiment I. Heat production increased with increasing density from 8.48 μW/insect at 1250 insects/200 g of wheat to 9.41 μW at 2500 insects/200 g of wheat and then decreased to 6.38 μW/insect at a density of 5000 insects/200 g of wheat (Fig. 1d). The mean heat production rates for density were significantly different at $P = 0.05$ (DMRT).

The effects of variable combinations (three-way interactions) on heat production are demonstrated in Fig. 2. Insect mortality for each test was less than 1%. At every moisture content of the experiment, heat production by all ages increased with increasing temperature from 15 to 35°C (Fig. 2a–c). Heat production was highest in four-week old adults at every combination of temperature and moisture content, and it produced much more heat than either age at 25°C in wheat of 15 and 18% MC. Heat production by each density also increased with increasing temperature at all moisture contents (Fig. 2d–f). At 18% MC, the heat production by 5000 insects appeared to be a linear function of increasing initial grain temperature from 15 to 35°C (Fig. 2f).

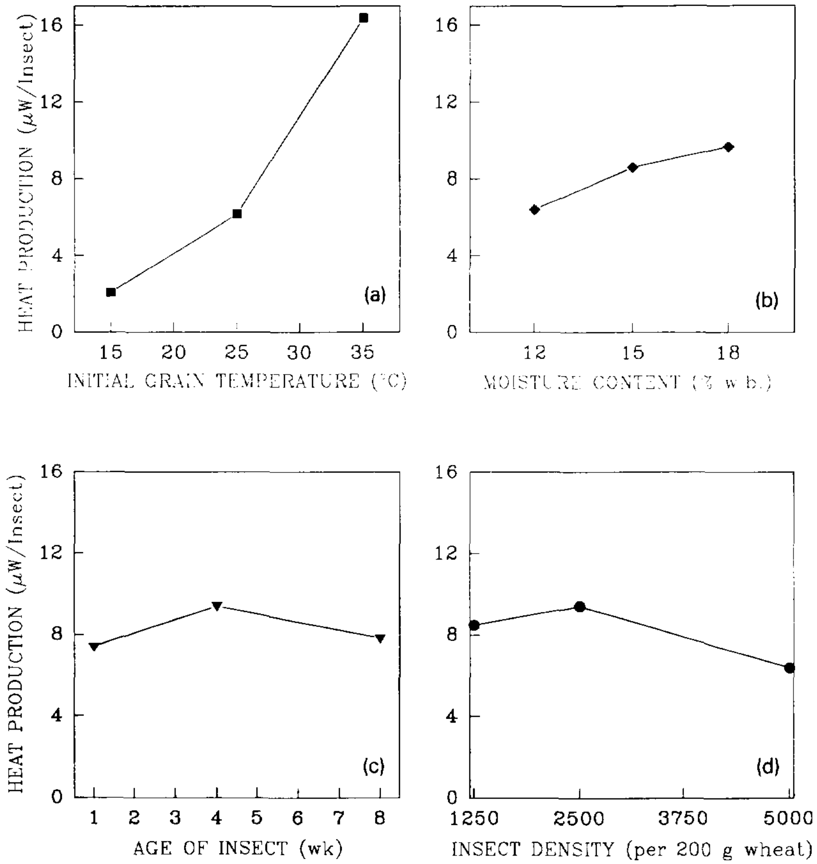

Fig. 1. The main effects of temperature (15–35°C), MC (12–18% WB), adult age (one–eight weeks old), and population density (1250–5000 insects/200 g of wheat) on the heat production ($n = 4$) of *C. ferrugineus*.

Effect of temperature increase on heat production

Instantaneous heat production rates measured during the test at initial grain temperatures of 15°C were not markedly affected by the temperature rise of the grain in the adiabatic flask. The correlation coefficient between grain temperature and time at 15°C for both experiments was 0.99, indicating a uniform heat production rate during the test.

At 25°C, increasing grain temperature affected the heat production rates of one-week old adults at 15% MC and those of four- and eight-week old adults at 18% MC (Experiment I, Fig. 3b, c). In Experiment II, heat production rates of 1250 and 5000 insects/200 g of wheat increased with increasing grain temperature at all moisture contents during the test (Fig. 3d–f) while the heat production rate of 2500 insects/200 g of wheat was similar to that of the four-week old adults of Experiment I.

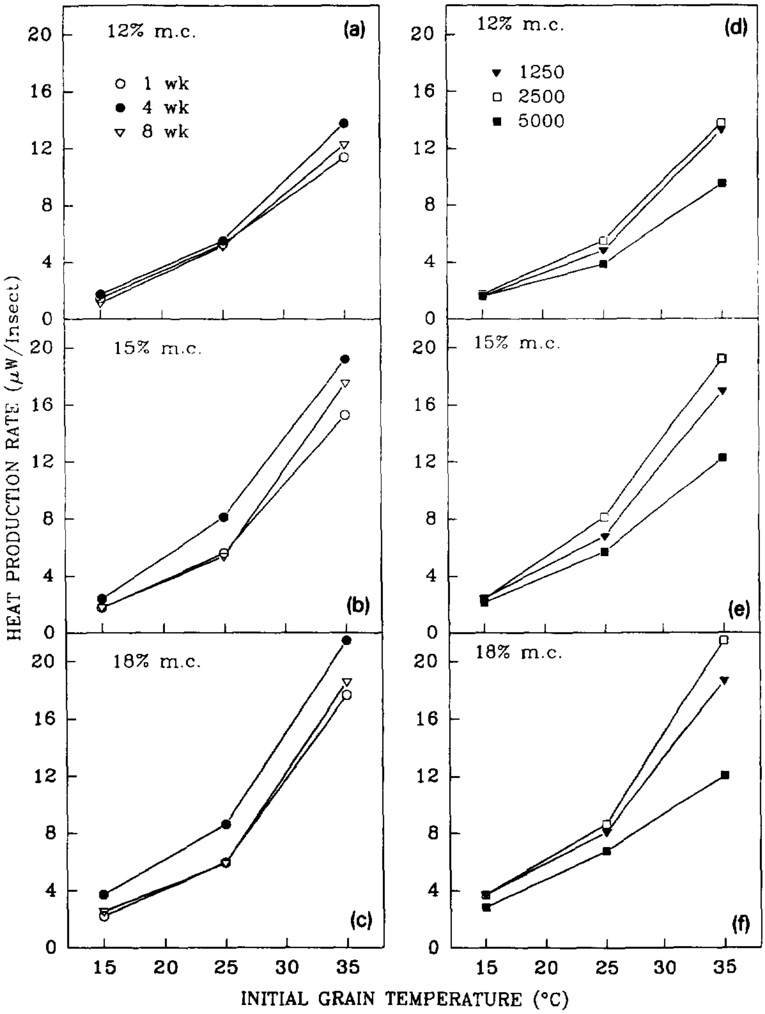

Fig. 2. The effects of initial grain temperature (15–35°C) and MC (12–18% WB) on the heat production (n = 4) of adult *C. ferrugineus* of different ages (at 2500 insects/200 g of wheat) and population densities (of four-week old adults).

At an initial grain temperature of 35°C, instantaneous heat production rates of all ages increased initially as the temperature of the grain in the adiabatic flask increased due to the heat production by the insects and then decreased or levelled off (Fig. 4a–c). The lowest heat production rate occurred with the youngest adults at all moisture contents. At 12% MC, heat production rates of the youngest and oldest adults increased initially with temperature and then decreased slightly, while the heat production rate of four-week old adults increased with increasing grain temperature to 37.5°C and then levelled off at a maximum of 13.53 μW/insect (Fig. 4a). At 15% MC, the heat production rate of the youngest adults decreased

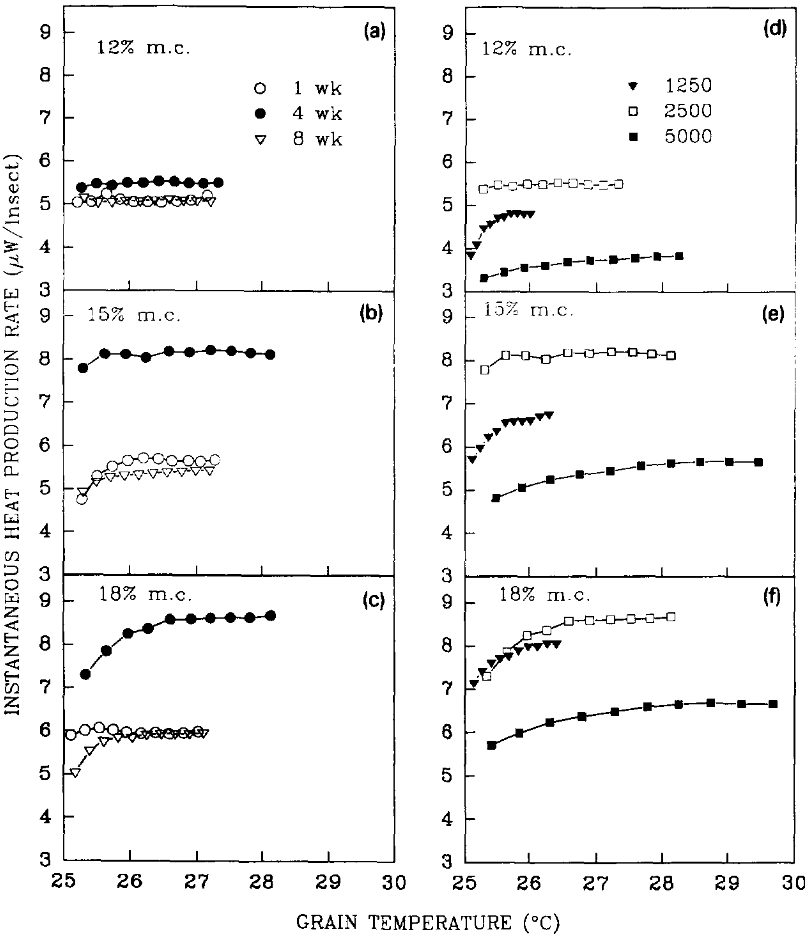

Fig. 3. The effects of temperature increase from 25°C and MC on the rate of heat production ($n = 4$) by adult *C. ferrugineus* of different ages (at 2500 insects/200 g of wheat) and population densities (of four-week old adults).

slightly after 37.2°C, whereas the heat production rate of four-week old adult increased steadily to a maximum of 19.82 μW/insect at 38.8°C and then decreased (Fig. 4b). The heat production rate of the oldest adults was initially higher than that of four-week old adults and it attained a maximum heat production rate of 18.97 μW/insect at 37.1°C and then decreased as grain temperature increased. At 18% MC, the heat production rate of the youngest adults increased initially with temperature to a maximum of 17.85 μW/insect, whereas the heat production rates of four- and eight-week old adults increased to maxima of 22.49 μW/insect at 38.6°C and 20.8 μW/insect at 37.1°C, respectively, and then decreased (Fig. 4c).

Instantaneous heat production rates at all densities were affected by increasing grain temperature from 35°C at all moisture contents (Fig. 4d–f), and the lowest

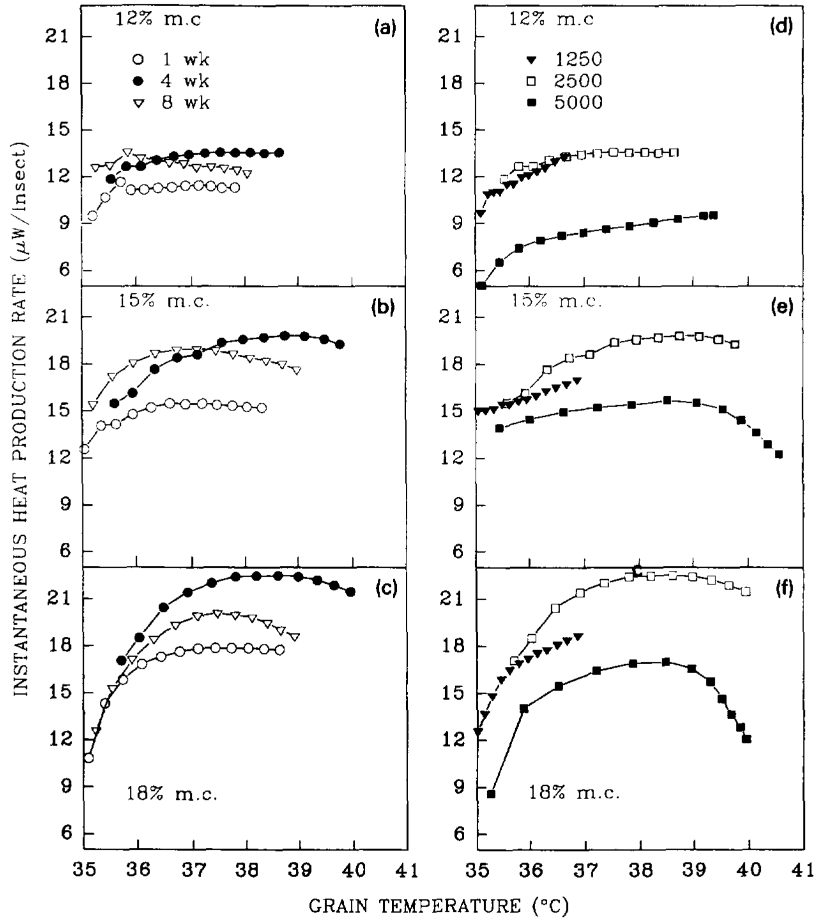

Fig. 4. The effects of temperature increase from 35°C and MC on the rate of heat production ($n = 4$) by adult *C. ferrugineus* of different ages (at 2500 insects/200 g of wheat) and population densities (of four-week old adults).

heat production rates per insect occurred at the highest density. At 12% MC, heat production rates by all densities increased with increasing grain temperature (Fig. 4d). At 15% MC, heat production rate per insect by the lowest density appeared to increase exponentially with increasing temperature from 35 to 36.9°C (Fig. 4e). Heat production rates per insect by intermediate and highest densities increased initially with increasing temperature and then decreased after 38.8 and 38.5°C, respectively. At 18% MC, heat production rate per insect by lowest density increased with increasing grain temperature whereas the heat production rates per insect by intermediate and highest densities followed the pattern described for 15% MC (Fig. 4f). Heat production rate of the highest density declined sharply from 16.97 μW/insect at 38.5°C to 12.01 μW/insect at 40.0°C (Fig. 4f).

4. Discussion

Heat production increased with increasing initial grain temperature because, as temperature increases, the energy of reactant molecules increases and exceeds the activation energy barrier, and thus the rate of reaction increases. Initial grain temperature effect on heat production followed the Q_{10} rule. Hoffman (1985) reported that Q_{10} factors of biological processes are generally between 2 and 4.

The effect of increasing moisture content was probably due to increased availability of water in the food substrate, and a reduction in kernel hardness which enabled the insects to feed more easily at the higher moisture contents. It is also possible that equilibrium relative humidity (ERH) adversely affected the heat production rate at 12% MC. The respective ERH at 15–35°C with 12, 15, and 18% MC is 48–57%, 70–76%, and 85–88%. As relative humidity increases, the saturation deficit of the air decreases, thereby reducing the evaporation of water from the insect body. The relative humidity (48–57%) in equilibrium with the grain at 12% MC is below the 70–75% required for optimum development by *C. ferrugineus* (Sinha and Watters, 1985). Surtees (1963) observed that *C. ferrugineus* locomotor activity was lower in wheat at 9% MC than in wheat at 14% MC and he suggested that inactivity of the insect in dry grain was due to the need to conserve body water.

The youngest adults produced the least heat probably due to the conversion of most of the energy intake for female oviposition. It is also possible that the youngest adults were not fully acclimatized to the stored grain environment and had not yet reached their maximum feeding potential. The high rate of heat production by four-week old adults was probably due to high biological activities like maintenance and motility, while eight-week old adults were less active physiologically than four-week old adults.

Instantaneous heat production rates by all ages and densities were not affected by an increase in grain temperature from 15°C. At 25°C, increasing grain temperature only slightly affected instantaneous heat production rates of some ages and densities during the test. Although an increase in grain temperature from 35°C caused an initial increase in instantaneous heat production rates, these rates attained a maximum and levelled off or decreased above certain grain temperatures. The oldest adult insect was affected most by increasing grain temperature as it attained the sharpest decline in heat production rates. Accumulated CO_2 (>9.0%) and depleted O_2 (<9.0%) in the flasks probably contributed to the decline in heat production rates at 15 and 18% MC. Wigglesworth (1972) reported that O_2 consumption by the larva of *Tenebrio molitor* (L.) begins to decline when the tension drops below 10% O_2 in the air.

The increase in heat production rate per insect with increasing density from 1250 to 2500 insects/200 g of wheat was probably due to the higher rate of temperature increase of the grain in the adiabatic flask at the higher density, and the subsequent increase in the rate of metabolism. The main reason for the lower heat production rate per insect at the highest density could be due to overcrowding and intraspecific competition which probably reduced their respiratory rates to conserve energy. The observations made at the highest density in this study are contrary to the suggestion by Smith (1966) that overcrowded *C. ferrugineus* adults at densities of 6400 and 26,400 insects/200 g of wheat would probably have higher metabolic rates than when they are not overcrowded. Flanders (1933) noted that the heat of respiration of *Sitotroga* larvae was greatest in jars with a density of 2–2.5 larvae per kernel and least in those with a density of 1, 3, or 4 larvae per kernel. Although the densities used in this experiment may represent extremely high infestations, such densities can be attained by *C. ferrugineus*. Kawamoto et al. (1989) simulated the population dynamics of *C. ferrugineus* and predicted that the beetle can reach 12,600 insects/200 g of wheat in 18 weeks at 30°C and 90% RH, and 10,200 insects/200 g of wheat at 30°C and 70% RH in the same time. Smith (1966) demonstrated that at densities of 6400 and 26,400 insects/200 g of wheat, the mortality of the beetles after 20 days at 30°C and 70% RH was only 9%, showing that mortality was not increased by such high levels of density.

The rate of increase in instantaneous heat production rate by the lowest density from 36°C was greater at 15% MC than at 18% MC indicating that the higher moisture content adversely affected insect respiration. The pattern of heat production rates by the intermediate density (Experiment II) with increasing grain temperature is similar to that of four-week old adults in Experiment I. Overcrowding, accumulated CO_2, and depleted O_2 in the flasks probably contributed to the sharp decline in instantaneous heat production rates of the highest density.

Although the grain in this investigation was better insulated than a pocket of grain in a grain bulk, nevertheless, the effect of temperature increase on heat production rates when the initial grain temperature was 35°C is indicative of what one might expect during insect heating in a grain bulk that is not being aerated. The observed trend of heat production rates decreasing above 37.5°C is similar to published accounts that an insect-induced hot spot reached a temperature of 37°C and then declined (Sinha and Wallace, 1966), that insect-induced heating raised the grain temperature to 38.5°C (Robertson, 1948), and that insects do not cause wheat to heat above 40–42°C (Oxley and Howe, 1944). Howe (1962) also demonstrated that a consequence of temperature rise in wheat infested with insects is a decrease in insect activity at higher temperatures. Heat production rates began to decline when the grain temperature exceeded 38°C, presumably because the temperature approached the lethal point of 42.5°C (Smith, 1965).

5. Conclusions

The heat production of adult *C. ferrugineus* under adiabatic conditions was significantly affected by initial grain temperature, moisture content, adult age, and adult population density. Increasing grain temperature caused an initial increase in heat production rates which reached a maximum or decreased as grain temperature increased. The data obtained from the present study can be used to simulate *C. ferrugineus* grain heating and hot spots in stored wheat.

Acknowledgement

We are grateful to the Natural Sciences and Engineering Research Council of Canada for providing financial assistance for this project.

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