INFLUENCE OF WHEAT CULTIVAR, TEMPERATURE, AND *THEOCOLAX ELEGANS* (HYMENOPTERA: PTEROMALIDAE) ON *RHYZOPERTHA DOMINICA* (COLEOPTERA: BOSTRICHIDAE) DEVELOPMENT

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MICHAEL D. TOEWS

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Thesis Approved:

Russell Wright for Gerrit Cuperus
Thesis Advisor, Gerrit W. Cuperus

Phillip G. Mulder, Jr.

Richard Berberet

Thomas A. Phillips

Mark E. Payton

Wayne B. Powell
Dean of the Graduate College

PREFACE

The first chapter of this thesis is a literature review focused on issues in stored wheat. Also included in chapter one is a review of the lesser grain borer, the parasitoid *Theocolax elegans,* and interactions among the trophic levels in my research. Subsequent chapters are formal papers representing my M.S. research project and are written in compliance with the publication policies and guidelines for manuscript preparation with the Entomological Society of America.

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Introduction

Grain production in the United States is a multi-billion dollar industry. After harvest, grain is often stored in both grower-owned bins and in commercial grain management facilities. Bulk grain storage provides an ideal habitat for a number of insect species. These insects, if improperly managed, continue to infest grain throughout storage and distribution to processors and eventually can result in reduced marketability. Traditionally, chemical insecticides were used to control storage insect infestations; however, domestic users and importing countries are imposing more restrictions on pesticide residues in cereal products. New methodologies need to be developed to control stored product insect infestations.

Pest Impacts on Stored Grain

Since the late 1980's wheat production in the U.S. has averaged over 2.1 billion bushels annually (USDA 1996). From 1990 to 1995, an average of 1.6 billion bushels of each harvest was being stored in December of each year (USDA 1996). A survey of Oklahoma grain producers and elevator managers found that both groups ranked insects as their greatest storage problem (Cuperus et al. 1990, Kenkel et al. 1994). Aside from direct feeding, insects also damage grain by contaminating it with cast skins, fecal material, webbing, and body parts. Insect feeding in stored grain can also contribute to lower test weights and the presence of musty odors. In addition, these conditions favor development of fungi, including some that produce mycotoxins. Each of these conditions results in a reduction in grain value. In order to maintain the confidence of processors and consumers, the industry must find and implement effective new methodologies to manage these constantly evolving insect populations.

Insect populations in most grain storage facilities are controlled through the use of insecticides. Numerous residual insecticide applications and fumigations occur throughout transportation and storage processes (Cuperus et al. 1990). These treatments result in reduced profitability and increase the risk of worker exposure hazards. In 1995, 71% of all wheat sampled from domestic grain elevators and storage facilities had malathion residues present, 54.2% had chlorpyifos-methyl residues, and 19.5% had chlorpyifos residues (USDA 1995). Recent samples of grain destined for export indicated that 85 to 95% of the samples had chlorpyrifos-methyl and/or malathion residues. Meanwhile, many countries that import wheat generally specify they want no pesticide residues. In addition, foreign and domestic consumers, flour millers, and breakfast cereal manufacturers are moving toward more stringent standards for kernel uniformity, grain cleanliness, falling number, wet gluten, extraction, and other end-user characteristics (Kenkel et al. 1994, Kenkel 1997).

Complications added to insect control procedures in grain management include pest resistance to insecticides, public concerns over food safety, and cancellation of registrations for grain protectants. Insecticide resistance is becoming an increasing problem. Resistance to long used protectants, such as malathion, is widespread and numerous (Zettler & Beeman 1995). Resistance to chlorpyrifos-methyl, pirimiphos-methyl, and dichlorvos is a recent development. A recent survey of attitudes indicated that over 70% of respondents were concerned with pesticide residues in produce (Collins et al. 1992). In addition, the Environmental Protection Agency is currently reviewing the toxicity of widely used protectants and fumigants such as malathion, methyl bromide, and dichlorvos. Methyl bromide, the fumigant of choice for some applications, will have

registered uses discontinued in January 2010 as called for in the 1987 Montreal Protocol on Substances that Deplete the Ozone Layer. The Clear Air Act in the U.S. calls for elimination of methyl bromide by January 2001. In addition, the 1996 Food Quality Protection Act will likely result in the loss of registrations for stored products insecticides such as the organophosphates.

Grain infested by insects, such as lesser grain borer, *Rhyzopertha dominica* (F.), will develop a number of problems directly affecting the official grade. Reduced quality grain will often have a high insect damaged kernel (IDK) count and elevated levels of dust and/or fecal matter, thereby decreasing the overall value of the grain. Lesser grain borer damaged wheat can result in lighter test weight, a reduction in germination when used as seed, and opportunities for other insect species to infest the grain. Insects at high density can impart "commercially objectionable foreign odors" (COFO) resulting directly in the U.S. "sample grade designation," the lowest possible grade. The sample grade designation results in grain suitable for only uses outside the food channel (Anderson et al. 1989). Lesser grain borers are noted for their ability to cause a characteristic sweet, musty odor when present at high infestation rates. Aside from direct feeding damage to seeds, insect infestations can raise the moisture content in small areas throughout the grain mass thereby increasing the incidence of mold problems.

End uses for grain infested with insects are quite limited. While the sample grade designation prevents usage in human food, it does allow for other uses such as livestock feed. Wheat infested with lesser grain borers also adversely affects parameters associated with animal feeding including food intake, body weight gain, food efficiency ratio, protein efficiency ratio, nitrogen absorption, biological value, net protein utilization and

dry matter digestibility (Jood & Kapoor 1992). If infested grain is still fit for human consumption, by FGIS standards, it is undesirable by end-product users. When bread is made from lesser grain borer infested wheat, the bread has decreased dough stability, dough development time, bread volume, and has an offensive odor (Sanchez-Marinez et al. 1997). Flour yield from infested wheat may also be significantly lower (Liscombe 1962, Sanchez-Marinez et al. 1997). Infested grain can also have increased insect fragment counts and ash levels resulting in a lower flour grade (Liscombe 1962).

IPM and Biological Control in Stored Grain

The stored grain industry is being challenged to implement a biointensive integrated pest management (IPM) system. The IPM concept is defined by Pedigo (1996) as "a sustainable approach to managing crop pests, using a combination of biological, cultural, and chemical tactics that reduce pests to tolerable levels that minimize economic, health, and environmental risks." Typical IPM programs in stored grains include integration of sanitation, temperature control through aeration and turning, residual pesticides, moisture control through drying, grain cleaning, grain leveling, biological agents, and fumigants. Monitoring for pest populations is an essential part of the program. Control measures are employed only when potential losses due to the pest population are greater than the cost of control (Cuperus et al. 1993). The objectives are to maintain grain quality, while minimizing both worker exposure and operating costs.

Grain inspection in the U.S. is conducted by three government agencies. The Grain Inspection, Packers and Stockyards Administration (GIPSA) is responsible for inspection and grain grading based on previously established standards. The Food and Drug Administration (FDA) is the regulatory agency responsible for insuring that the

domestic food supply is safe. The FDA has authority to prevent grain with too many insect damaged kernels, mycotoxins, or pesticide residues from reaching the food supply. These two agencies work together under a memorandum of understanding in situations where both organizations are involved. Finally, prior to export, grain must have a phytosanitary certificate issued by the Animal and Plant Health Inspection Service (APHIS). Certification ensures the importing country that the commodity is free from quarantine and injurious pests.

Parasitoids are often found in stored grain environments and are reported to parasitize most of the important insect pests (Hagstrum & Flinn 1992). In the past, all insects detected in stored grain were counted as pests and judged to be deleterious to grain quality. Parasitoids and predators can now be legally released into stored grain, stored legumes, and structures (Anonymous 1992). Parasitoids and predators are subject to regulation by the Federal Insecticide Fungicide and Rodenticide Act (FIFRA) but are exempt from tolerance requirements in food products. This has increased interest in using entomophagous insects, such as the parasitoid *Theocolax elegans* (Westwood) (Hymenoptera: Pteromalidae), in managing insects that damage stored grain. Results of the first large scale test of parasitoids (including *T. elegans*) released into bulk stored grain suggested that they could control populations of stored grain pests including lesser grain borers (Parker and Nilakhe 1990). These experiments also indicated that introducing parasitoids into stored grain reduced the number of insect-damaged kernels below that of grain treated with chemical protectants.

Biological control methods can be divided into three groups including: importation and introduction of a new species, augmentation of beneficial species by

mass rearing and periodic colonization, and conservation of natural enemies by manipulation of the environment to make conditions more suitable for their survival (Debach & Rosen 1991). Each of these has been successfully demonstrated using different parasitoid species. My research makes use of the augmentation mode of natural enemy or parasitoid enhancement.

Numerous scientists have conducted postharvest host resistance studies to lesser grain borer with a range of wheat germplasm (Bhatia & Gupta 1969, Singh & Mathew 1973, Phadke & Bhatia 1975, Amos et al. 1986, Sinha et al. 1988, McGaughey et al. 1990, Cortez-Rocha et al. 1993). However, only recent studies utilized *T. elegans* as a parasitoid of lesser grain borers (Flinn et al. 1994; Flinn et al. 1996, Flinn 1998). *T. elegans* has been cited as a possible biological control organism for the maize weevil, *Sitophilus zeamais* Motschulsky, in stored corn (Williams & Floyd 1971a, 1971b, Sharifi 1972, Wen et al. 1994). Unfortunately, very few of these past studies utilized wheat cultivars available for the present study. This study was the first such attempt to scrutinize the interrelationships among these organisms on an array of wheat cultivars commercially grown in the U.S.

Breeding plants for resistance to insects in postharvest storage is not commonly done by commercial and non-commercial breeders. This arena has recently gained interest from researchers using molecular techniques. However, insertion of genes into the plant that reduce the activity of insects in postharvest storage is still a novel idea. Pueyo et al. (1995) showed the ability of a proteinaceous inhibitor from *Phaseolus vulgaris* L. (Leguminosae) to be effective *in vitro* against α-amylases of the red flour

beetle, *Tribolium castaneum* (Herbst). They demonstrated this technique by adding 1% of the inhibitor to a diet consisting of wheat flour plus germ. The mixture slowed the development of *T. castaneum* larvae. However, the inhibitor was not effective when tested against lesser grain borer. Zhu et al. (1996) demonstrated that an *N-acetylglucosamine*-specific lectin gene from *Griffonia simplicifolia* (Leguminosae) had insecticidal properties to the cowpea weevil, *Callosobruchus maculatus* (F.).

***Triticum aestivum* L.**

All currently grown cultivars of U.S. wheat (*Triticum aestivum* L. and *T. turgidum* L. var *durum*) have been selected from introduced germplasm. This process has taken place in roughly two distinct time periods. The first extends from the arrival of settlers in North America to the early part of the twentieth century when many European cultivars were introduced. The second period has taken place in the past 100 years and includes all germplasm introduced through formal wheat breeding programs.

During the first period, hexaploid wheats, brought to the U.S. from Europe, were very heterogeneous and did not yield particularly well (Cox 1991). Cox and Worrall (1987) detected 35 different gliadin electrophoretic patterns in 11 strains of the exact same cultivar maintained at various locations. Gliadin proteins are those proteins soluable in ethanol. This heterogeneity within a cultivar makes it difficult to quantify the presence of characteristics in these old lines of germplasm. The introduction of 'Turkey' wheat by Mennonite settlers marked the beginning of hard winter wheat in the U.S.. However, even 'Turkey' was so variable that it and closely related cultivars, such as 'Kharkof' and 'Crimean', had sufficient genetic diversity to serve as parentage for the

majority of many hard winter wheat cultivars for over 50 years (Schmidt 1974, Cox 1991).

Cox (1991) traced the contribution of introduced germplasm to the development of U.S. wheat cultivars. He found that a narrow range of founding germplasm accounted for a large portion of current cultivars. His study of pedigrees for 224 cultivars, all released before 1975, found that 69% were from parentage directly linked to founding germplasm. The introduction of 'Mediterranean' made major ancestral contributions to the soft red winter, hard red spring, and white classes of wheats. The most striking example occurred with the popular 'Turkey' cultivar; it was used as a major ancestor of all modern U.S. wheat classes except the durum class.

Current projects working on germplasm enhancement include the work of wheat breeding programs across the country by United States Department of Agriculture (USDA) researchers, university personnel, and private companies. These is constant pressure to develop new germplasm since few of the early wheat cultivars provided resistance to evolving production problems including insects, foliar diseases, and lodging. The increase in fertilizer use has also prompted the need for new germplasm. As a result of this demand, 75% of cultivars released after 1975 have additional germplasm introduced in their pedigree (Cox 1991).

Cultivars are grouped according to the season when they are planted as either winter wheat or spring wheat. Classification into the six major classes of wheat are based on the parameters related to milling and baking (Krischik et al. 1995). The six classes of wheat are hard red winter, soft red winter, hard red spring , durum, soft white, and hard white. While kernel size is largely related to cultivars, most cultivars within each class

have general similarity in size. Within a cultivar, kernel size differences are a result of kernel positioning on the plant (Kirby 1974, Simmons & Moss 1978). Class differences determine the end use of the wheat. Hard wheat classes are used in the production of bread while soft wheats generally are used in the baking industry for pastries and crackers. Durum wheats are used to make pasta products.

***Rhyzopertha dominica* (F.)**

The lesser grain borer, *Rhyzopertha dominica (*F.), is a serious pest of stored products and considered to be native to India (Schwardt 1933, Potter 1935). While this beetle has adapted to feeding on stored products, the majority of species in the Bostrichidae family are wood borers (Borror et al. 1989). Due to its affinity for exported stored products such as vegetable products, cereals, and baked goods, lesser grain borer is cosmopolitan in its distribution (Potter 1935). During World War I, large numbers of these insects were transported to the U.S. in wheat from Australia (Schwardt 1933).

Lesser grain borer adults have a voracious appetite for either intact or damaged kernels and feed in grain as both larvae and adults. Golebiowska (1969) found that adults fed more intensively before egg laying and thus created more damaged kernels possibly enabling increased larval survival. Eggs are laid singly or in small clusters exterior to the kernels. Opinions vary regarding ability of newly hatched larvae to penetrate undamaged kernels, as damaged kernels are often preferred by larvae. Although larvae can develop outside the kernel in wholemeal flour, developmental time is shorter when development occurs within the grain (Howe 1950). Larvae molt 3-5 times depending on environmental conditions and food sources. Developmental times from egg to adult average 25 days at

34.0° C and 70% RH (Birch & Snowball 1945, Howe 1950). Optimal developmental temperatures are 32-35.0° C (White 1995). A lower temperature such as 28.0° C, at 70% RH, will lengthen the average developmental time to 37 days (Howe 1950). Likewise, temperatures above 34.0° C slow the development. Exposure to temperatures above 39.0° C completely halt oviposition (Birch 1945b).

Daily fecundity by female lesser grain borers is erratic. Golebiowska (1969) found that over a period of four weeks egg production began at high levels after beetles infested a grain mass, then declined rapidly during the first week. The ovipositional rate then increased again during the second and third weeks before ultimately decreasing to a very low level during the fourth week. Howe (1950) reported average egg production per female was 244 eggs. When both sexes are present in the grain mass, large quantities of frass are produced prior to egg laying. However, when only females are present this behavior is not observed. Not all eggs hatch, as they are frequently damaged by adults in the process of oviposition and/or by activity of adult beetles immediately thereafter (Schwardt 1933). Predacious mites also contribute to egg mortality.

***Theocolax elegans* (Westwood)**

A member of the Pteromalidae, *T. elegans* has been investigated as a potential biological control agent for lesser grain borer. First described in by Westwood (1874), *T. elegans* was thought to be of little importance as a parasitoid. In 1919, a short description of the parasitoid concluded that, "This feeble species seems of no importance in controlling its hosts" (Birdwell 1919). Goodrich (1921) later published similar statements in reference to *T. elegans*. Boucek (1988) reviewed this species and placed it

in the genus *Theocolax*, formerly known as *Spalangiomorpha*, *Cercocephala*, and *Choetospila*. Although *T. elegans* principally occurs on the granary weevil, *Sitophilus granarius* (L.), maize weevil, *Sitophilus zeamaize* Motschulsky, and rice weevil, *Sitophilus oryzae* (L.), Bare (1942) noted that the parasitoid could also live on other hosts such as the cigarette beetle, *Lasioderma serricorne* F. The first record of this parasitoid attacking lesser grain borer larvae was published in 1921 (Herdman 1921). *T. elegans* also can complete development on a variety of other beetles (Van den Assem & Kuenen 1958).

Theocolax elegans is very small (0.7-2.1 mm) and strongly resembles an ant. Its body is colored with a shiny opaque black sheen; the forewings are clear except for a narrow pigmented bar centered between the leading trailing edges of the forewings. The parasitoid is a solitary ectoparasitoid with a strong preference for 3rd and 4th instars of its hosts (Sharifi 1972). Reproduction is of the arrhenotokous type (Williams & Floyd 1971a) meaning that the male offspring are haploid and female offspring are diploid. Many adults of the Pteromalidae practice host feeding (Clausen 1962) but it has never been reported by *T. elegans*. Host feeding is a behavior where the adult female first stings the prey and then secretes a "feeding tube" around the ovipositor and into the body cavity of the prey. The wasp then ingests hemolymph from the host through the feeding tube. This behavior is theorized to provide needed protein for oogenesis. After oviposition in close proximity to the larva of *R. dominica,* the parasitoid larva hatches and attaches to the dorsal body wall of the host larva and feeds as an ectoparasite. Only 10 days are required for egg through larval development at 25.0° C (Van den Assem &

Kuenen 1958). However, 8 to 11 additional days are needed before adult emergence occurs (Bare 1942, Van den Assem & Kuenen 1958). Average lifespan of an adult wasp is 2 to 3 weeks at 30.0° C.

All hosts attacked by *T. elegans* occur inside kernels of grain. Therefore, it is of utmost importance that the parasitoid be able to locate and oviposit on kernels containing grain borers. Van den Assem & Kuenen (1958) indicated that adult *T. elegans* can differentiate between "clean" grain masses and grain masses with host larvae present. Once the infested grain mass has been located the female begins to search for infested kernels by vibrating her antennae on each kernel. If a kernel contains a 3rd or 4th instar lesser grain borer, the vibrating becomes intense and is termed "drumming." The drumming is concentrated on a specific portion of the surface of the kernel where the wasp then oviposits. This process is quite accurate in determining the position of larve within kernels.

Sometimes host larvae occur outside the kernels but this is not as common as development within the kernel. In the rare instance that a female parasitoid finds a host out side of the kernel, she will simply inspect the larva and move on. This behavior indicates that the ovipositional stimulus is the larva within the kernel (Van den Assum & Kuenen 1958). While the possibility that *T. elegans* uses olfactory cues has not been ruled out, it is obvious that the tactile abilities of the antennae are an important determinant in site selection for oviposition. Perhaps the size of the larger 3rd and 4th instar host produces a different "feel" or sound in response to the drumming that initiates

oviposition. More common methods of host finding by entomophagous insects, such as optical cues and temperature, may not be effective in stored grain environments.

Few studies have been conducted to assess the utility *T. elegans* in regulating populations of lesser grain borer. Flinn et al. (1996) conducted an experiment, over two consecutive years, in steel grain bins where *T. elegans* suppressed lesser grain borer populations in excess of 90% compared with control bins. Furthermore, *T. elegans* suppressed the pest population well below the FGIS standard for sample grade wheat. In a second experiment Flinn (1998) demonstrated that augmentative releases of *T. elegans* were more efficacious when coupled with cooler temperature compared to the optimal temperature for reproduction by lesser grain borers.

Effects of Temperature on *T. elegans*

Flinn (1998) showed that suppression of lesser grain borer populations by *T. elegans* significantly increased at 25.0° C when compared to suppression at 32.0° C. In a study conducted with another member of the Pteromalidae, *Anisopteromalus calandrae* (Howard), total progeny, net reproductive rate, and intrinsic rate of increase were greater with increasing temperatures from 20.0° C to 35.0° C (Smith 1992). However, the generation time and life expectancy decreased as temperature was increased. Research using another parasitoid found in stored grain, *Cephalonomia waterstoni* (Gahan) (Hymenoptera: Bethylidae), showed that the number of paralyzed larvae increased with temperature from 20.0° C to a peak at 30.0° C (Finn 1991

Williams & Floyd (1971b) found that *T. elegans* adults cannot survive subfreezing temperatures for more than a few hours. Although larvae can withstand cold

temperatures better than adults, even larvae experienced a 90% increase in mortality after 10 days of subfreezing conditions. No research has been conducted on the effects of high temperature with *T. elegans.*

In the southern U.S., temperature in a grain storage facility often is unregulated, unless aeration is employed to cool the grain as part of an IPM program. Aeration is accomplished by forcing cooler air through a grain mass using electric fans. The reduction in grain temperature can directly affect the ability of insects to reproduce in the grain mass (Cuperus et al. 1986, Kenkel et al. 1994). Temperature fluctuations could be even more important in the future if managers wish to enhance effectiveness of biological control via species such as *T. elegans*. Grain moisture can also have an effect on the intrinsic rate of increase of the pest species (Birch 1945a, 1945b). Storage facilities are usually fitted with equipment that enables the manager to manipulate moisture and temperature of the grain through turning, blending, aeration, or chilling. These practices increase the potential for effective pest management.

Tritrophic Interactions and Resistance

The management system of concern in this thesis can be viewed as an interaction among components in an ecosystem with three trophic levels (Lindeman 1942). The stored grain is equivalent to the primary producer of natural ecosystems. The lesser grain borer is equivalent to the primary consumer, and *T. elegans* represents the third trophic level or secondary consumer. Interactions among these three trophic levels are collectively termed 'tritrophic interactions.' An important observation in tritrophic interactions is that members of the first and third trophic levels may act in a mutualistic manner where both species benefit from the association (Read et al. 1970, Price 1986). A

working knowledge of interactions among these trophic levels is important. Starks et al. (1972) studied relationships in a cereal ecosystem and quantified important observations pertinent to other ecosystems. Principal in their study was the concept that the primary trophic level, i.e. the host plant of the herbivore, could influence the third trophic level, or natural enemy of the pest (Starks et al. 1972, Reed et al. 1991, 1992, 1993). A second important aspect of these studies was that the third trophic level, the parasitoid, can decrease damage to the first trophic level.

Plants exhibit resistance to herbivores through antibiosis, resistance, and antixenosis (Painter 1951, Kogan & Ortman 1978). 'Antibiosis' describes the adverse effects by the plant on the herbivore's life history, while 'tolerance' describes the ability of the plant to withstand feeding by the herbivore. 'Antixenosis' describes plants unsuitable for use by the herbivore, which therefore avoids the plant. Past research has shown that plants exhibiting antibiosis at the second trophic level, seemed also to have deleterious affects to organisms at the third trophic level (Reed et al. 1991, 1992, 1993). In comparison, plants tolerant to the second trophic level of activity permitted greater species populations at the third trophic level (Reed et al. 1993).

Objectives

This study was carried out in two separate parts. The first study was conducted to determine relative levels of host resistance to the lesser grain borer among eight U.S. cultivars of wheat stored at two temperatures. The specific objectives were (1) to compare yield of adult lesser grain borer progeny in eight wheat cultivars; (2) compare the effects of temperature on the yield of lesser grain borer progeny; (3) correlate levels

of progeny production by lesser grain borers with physical and chemical characteristics of wheat cultivars; (4) assess the effect of wheat cultivar on weights of adult progeny.

The second study was conducted to (1) evaluate the effects of wheat cultivar, temperature, and the parasitoid *T. elegans*, on adult progeny yield of lesser grain borers; (2) examine interactions among the three trophic levels; (3) determine percent suppression in progeny yield of lesser grain borer adults due to both temperature and cultivar; (4) compare the ability of the parasitoid to complete its life cycle under the influence of different temperatures; (5) use single kernel characteristics to relate potential efficacy of *T. elegans* at suppressing lesser grain borer progeny.

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CHAPTER 2

SUSCEPTIBILITY OF EIGHT U.S. WHEAT CULTIVARS TO INFESTATION BY LESSER GRAIN BORER, *RHYZOPERTHA DOMINICA* (F.), (COLEOPTERA: BOSTRICHIDAE)

Abstract

Wheat cultivars were assessed to determine their respective level of resistance to lesser grain borers in postharvest storage. Cultivars were representative of hard red winter, soft red winter, white spring, and durum wheat classes currently grown in the United States. Samples of each cultivar were maintained at 30.0° C and 70% RH and infested with two to three week old adult beetles for one week. Following this one week ovipositional period, adult beetles were removed and their progeny allowed to complete one life cycle. Two temperatures, 27.0° C and 34.0° C, were studied to examine the role of temperature (calculated in degree days) in development. This experiment was repeated two additional times under similar conditions. Cultivars harboring a large quantity of progeny were considered more susceptible than those cultivars where fewer progeny completed their life cycle. Each cultivar was analyzed for single kernel properties such as hardness, protein, and diameter. Wheat cultivar had a significant influence on quantity of progeny in all experiments. There were no significant effects on progeny size due to temperature. Cultivars with smaller kernels were more susceptible to development of larger generation sizes in Experiment 1 but not in the other two experiments. A forth experiment using large and small kernels from the same cultivar suggested that larger quantities of progeny are produced on small kernels compared to large kernels. Individual beetle weights were not influenced by temperature or cultivar.

Introduction

The United States is a major grower of hard, red winter and spring wheat, *Triticum aestivum* L., and stores 1 billion bushels (Kenkel et al. 1994) of the estimated 2.1 billion bushels harvested each year. The primary purpose of grain storage is to increase the net value of the crop by holding grain until prices are more favorable (Anderson et al. 1995). However, storing grain can also cause the overall quality of the commodity to decrease, thereby offsetting positive economic returns. Common storage problems include mold and insect infestations (Cuperus et al. 1990). A survey of elevator managers in 1987 and 1993 determined that insects were perceived as their worst problem (Cuperus et al. 1990, Kenkel et al. 1994).

Wheat cultivars are developed for a wide variety of locations and applications in crop production. Improved cultivars are bred to increase resistance to diseases and insects, adapt to new environments, increase quantities of certain nutrients, change growth habits, and to increase productivity (Martin et al. 1976). Although increased yield is often the target of crop improvement, it is important that the commodity not be highly susceptible to pathogens or grain degrading components capable of negating any increases to net returns. Cultivars have different levels of resistance to stored product insects (Singh & Mathew 1973, Phadke & Bhatia 1975, Amos et al. 1986, Sinha et al. 1988, McGaughey et al. 1990, Cortez-Rocha et al. 1993).

The lesser grain borer, *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae), is a serious pest of stored wheat and is cosmopolitan in distribution (Potter 1935). The female lays eggs singly or in small groups exterior to the grain; eggs can be attached to a kernel or laid loosely in the grain. After hatching, the first instar immediately bores into

the kernel where it completes five instars. Lesser grain borers pupate inside the kernel before adults emerge and chew their way out of the kernels. This insect is extremely damaging because it feeds exclusively on the grain as both a larva and adult. Total developmental time averages 25 days at 34.0° C and 70% RH (Howe 1950). Optimum temperatures for development are 32-35.0° C (White 1995).

Plants exhibit resistance to the pest through antibiosis, tolerance, and antixenosis (Painter 1951, Kogan & Ortman 1978). 'Antibiosis' describes the adverse effects by the plant on an insect's life history, while 'tolerance' describes the ability of the plant to withstand infestation by the insect. 'Antixenosis' describes plants that are unsuitable for use by the insect and the insect therefore avoids the plant

In the southern U.S., temperature in a grain storage facility is often unregulated unless aeration is employed to cool the grain as part of an Integrated Pest Management (IPM) program. Aeration is accomplished by forcing cooler air through a grain mass using electric fans. The reduction in grain temperature can directly affect the ability of pest insects to reproduce in the grain mass (Cuperus et al. 1986, Kenkel et al. 1994). Temperatures employed in this experiment was intended to represent the effect of aeration on the grain mass.

In postharvest research the plant is actually represented by the kernel of grain instead of a green plant. Host resistance in this research relates to qualities of kernels that reduce infestation or damage by insects. This study was conducted to determine relative levels of host resistance to infestation by the lesser grain borer among eight cultivars of wheat when stored at two temperatures. The specific objectives were (1) to compare

yield of adult lesser grain borer progeny in eight wheat cultivars; (2) compare the effects of temperature on the yield of lesser grain borer progeny; (3) correlate levels of progeny production by lesser grain borers with physical and chemical characteristics of wheat cultivars; (4) assess the effect of wheat cultivar on weights of adult progeny.

Materials and Methods

Cultivar Resistance Test

Eight wheat cultivars were procured from commercial seed producers and various foundation seed stocks across the U.S. The cultivars selected represented divergent genetic lineages by representing cultivars from five major classes of wheat. Cultivars in the study included the hard red winter selections 'Triumph 64' and '2180' (Oklahoma Foundation Seed Stocks, Inc., Stillwater), soft red winter selections included 'Madison' (Arkansas Agricultural Experiment Station, Fayetteville) and 'Coker 916' (Novartis Seeds, Inc., Bay, Arkansas), durum cultivars were 'Munich' and 'Monroe' (North Dakota Seedstocks Project, Fargo), the hard red spring selection 'Newana' (Montana Foundation Seedstocks, Bozeman), and the white spring cultivar 'Wawawai' (Washington State Crop Improvement Association, Pullman). Following receipt, wheat was frozen for one week to eliminate the possibility of previous infestations. Seed was then cleaned with multiple passages over a seed cleaner (Clipper model M2B, Bluffton Agricultural Industrial Corp., Bluffton, IN). All experiments were conducted using subsamples of a single sample of seed. The bulk seed was stored in plastic bags at 10.0 C until used in experiments. Prior to each experiment, wheat was tempered to 13 ± 0.5% moisture content by adding water

or allowing ambient drying. Moisture contents were determined using the dry-weight method ASAE standard (Society of Agricultural Engineers 1996).

Before starting experiments, subsamples of each cultivar were analyzed at the Oklahoma State University Wheat Quality Laboratory (303 Agriculture Hall, Stillwater, OK 74078) for physical and chemical properties. Protein content was determined using the Kjeldahl method (American Association of Cereal Chemists 1983). Hardness measures were determined using both an NIR machine (Technicon InfraAlyzer model 400, Bran + Luebbe GmbH. Norderstedt, Germany) and a single kernel hardness (SKH) tester (Pertain Inc. Model 594, Springfield, IL). Average kernel weight, peak force required for crush, conductance, total force required for crush, time required to completely crush, and diameter were obtained using a single kernel hardness tester (Pertain Inc. Model 594, Springfield , IL). All measurements given by the hardness tester, except average weight and diameter, are unitless and therefore intended solely for comparison among cultivars within that parameter.

Experiments were conducted with 100 ± 1.0 g of wheat in 0.2366 liter glass canning jars. Fifty, 2-3 week old unsexed lesser grain borer adults, from stock cultures reared on the hard red winter wheat cultivar '2180', were introduced into each of 16 jars per cultivar. Ventilation was permitted through filter paper fitted into lids. All jars were initially held at 30.0 ± 0.5° C in one chamber for one week to allow a consistent opportunity for oviposition by adults in each jar. After the ovipositional time period, adult insects were removed by gently sieving the grain over a 1.40 mm standard sieve. Beetles were collected below on a 0.425 mm sieve, while the dust fell through both sieves

to be collected in a bottom pan. All grain and dust were returned to the jars. Equal numbers of jars of each cultivar were then placed in each of four upright environmental chambers (Model I-35 LVL, Percival-Scientific Corp., Boone, IA). Two chambers were set at 27.0 ± 0.5° C and two at 34.0 ± 0.5°C with 70 ± 5% RH. Hygrothermographs were maintained inside each chamber to monitor and record temperature and humidity for the duration of all experiments. Throughout the experiment, completely dark conditions were utilized.

A degree day model, developed by Subramanyam et al. (1990), was used to assure similarity in experimental protocol despite the differences in insect developmental time attributed to the different temperatures. The model used a threshold temperature of 13.2° C for egg to adult development of lesser grain borers. In this study insects were allowed 900 degree days to develop; adult progeny were collected at four intervals within the 900 degree days. Data analysis was performed only on the total number of progeny collected and not broken down by individual collection interval. Previous research (Toews unpublished) indicated that progeny took longer to develop on large kernels than on small kernels. However, after 900 degree days had elapsed, at least 98% of all progeny had emerged regardless of kernel size.

Layout of each experiment was a split plot arrangement where the main unit effect was temperature and the subunit effect was cultivar. Each chamber represented one application of 'temperature'. In order to increase the number of observations at the subplot level, 'cultivar' was replicated four times within each main plot. Therefore, experiment included two replications of temperature (two chambers at each temperature)

and 16 replications of cultivar (four replications within each of the four chambers). This experiment was conducted three times.

To determine if cultivar influenced beetle weight, adult weights were determined by collecting 30 beetles from Experiment 2 that were less than one week old. Beetles were frozen immediately after collection and stored until used. Specimens were cleaned for five minutes in an ultrasonic cleaner (model FS-30, Fisher Scientific, Pittsburgh, PA) filled with water. Clean and intact beetles from each jar were placed in groups of 20 and placed in 3 ml shell vials. Vials were placed in a laboratory oven (model 18A, Blue M, Blue Island, IL) at 130.0° C for 24 hours. Immediately before vials were removed from the oven, lids were placed on each vial. Vials were placed in a dessicator with aluminum oxide for 30 minutes before weighing on a microbalance (model M3P, Sartorius Corp., Bohemia, NY).

Kernel Size Test

Because Experiment 1 indicated that quantity of lesser grain borer progeny was related to kernel size, a separate experiment was conducted to assess the role of kernel size within a single cultivar. A hard red winter wheat, '7853', was obtained directly from a local grower. Individual kernels were separated into two size groups using slotted hand sieves; slot length of each sieve was 19.05 mm. Large kernels were collected between a 3.18 mm and a 2.78 mm sieve; small kernels were collected between a 2.38 mm and a 1.98 mm sieve. The two kernel sizes were the treatments for this experiment. Both kernel sizes were then tempered to 13.0% moisture content.

The experimental design was a randomized complete block with four subsamples of the two treatments per replication; there were nine replications of the treatments. The entire experiment was located on a centered shelf in an upright environmental chamber (Model I-35 LVL, Percival-Scientific Corp., Boone, IA). Throughout the experiment, environmental conditions were held constant at 34.0 ± 0.5° C and 70 ± 5% RH.

In each of 72 jars, 40 unsexed adult lesser grain borers were placed on 75 ± 1.0 g of wheat for an ovipositional period of four days. Following the ovipositional period, adults were removed and their progeny allowed to mature for six weeks at which time progeny were collected, counted, and analyzed.

Data Analysis

Data for all experiments were analyzed using PC-SAS version 6.11 (SAS Institute Inc. 1994). Before statistical analysis, all progeny counts were transformed using a square root transformation (Zar 1984) to correct for heteroscedastic data. Treatment means were analyzed using PROC GLM (SAS Institute Inc. 1994) and separated using the LSD method (Steel & Torrie 1980) at the α=0.05 level. Regression data with mean kernel characteristics and mean progeny production were made using PROC REG (SAS Institute Inc. 1994).

Results

Cultivar Resistance Test

Raw data from the analyses of individual wheat cultivar parameters are summarized in Table 1. Hardness values, obtained by both the NIR and SKH methods, varied widely among cultivars. 'Coker 916' had a NIR value of 26.3 while 'Munich' had

a 179.8. Percent protein, the only chemical property measured, varied from 10.6% ('Coker 916') to 16.7% ('Triumph 64'). The values for kernel diameter ranged from 1.8 ± 0.3 mm in 'Triumph 64' to 2.5 ± 0.5 mm in 'Wawawai'.

Numbers of progeny produced were greatest in Experiment I (Fig. 1). In Experiment 1, the main plot comparison, temperature, did not contribute significantly to differences in number of progeny ($F = 3.57$; df = 1, 2; $P = 0.1993$). However, the subplot comparison, cultivar, was significant ($F = 3.01$; df = 7, 98; $P = 0.0066$) (Table 2). 'Triumph 64' and 'Coker 916' produced more progeny than the remaining cultivars except 'Monroe'. The difference between the cultivar 'Triumph 64', in which the most beetles were produced, and that with the least, 'Wawawai', was nearly two fold.

Progeny production from Experiment 1 was analyzed using linear regression of cultivar parameters, the independent variable, to predict progeny production, the dependent variable. Parameters found to predict progeny numbers most accurately in Experiment 1 were average kernel weight, average length, and average diameter (Table 3). However, further investigation revealed that average weight was highly correlated with average diameter ($F = 110.150$; df = 1, 6; $P = 0.0001$; $R^2 = 0.9483$; n = 8), average area ($F = 6.843$; df = 1, 6; $P = 0.0398$; $R^2 = 0.5328$; n = 8), and length of crush ($F = 16511.009$; df = 1, 6; $P = 0.0001$; $R^2 = 0.9996$; n = 8). These characteristics all describe the physical size of the kernel. All other kernel characteristics were nonsignificant in relating number of lesser grain borer progeny.

In Experiment 2, temperature was not a significant factor ($F = 1.57$; df = 1, 2; $P = 0.3369$) in progeny production. At the subplot level, cultivar was a significant factor ($F =$

11.79; df = 7, 98; $P = 0.0001$). The cultivars 'Coker 916' and 'Monroe' harbored the greatest number of progeny. Less progeny emerged from 'Newana' than any other cultivar. These results are summarized in Table 4. None of the cultivar parameters in Experiment 2 were correlated significantly with number of lesser grain borer progeny (Table 5).

Weights of adult dried beetles from Experiment 2 were not significantly different between temperatures ($F = 0.62$; df = 1,2; $P = 0.5145$) or among cultivars ($F = 0.96$; df = 7,84; $P = 0.4629$). Mean weights for 20 beetles ranged from 7.964 ± 0.171 mg in 'Newana' to 8.494 ± 0.197 mg in 'Coker 916' (Table 6).

Progeny production from Experiment 3 was similar in magnitude to Experiment 2. In Experiment 3, temperature was not a contributing factor to variability in progeny numbers ($F = 0.17$; df = 1, 2; $P = 0.7193$). There were significant differences in progeny numbers attributable to cultivars ($F = 4.19$; df = 7, 98; $P = 0.0004$). 'Munich', 'Monroe', and 'Coker 916' harbored the most progeny while 'Madison' and 'Newana' harbored the fewest (Table 7). Similar to Experiment 2, no significant relationships were detected between any of the single kernel characteristics or cultivar parameters and progeny size (Table 8).

Kernel Size Test

Results from the test on kernel size indicated that numbers of lesser grain borer progeny were marginally larger when reared on small kernels in comparison to those reared on the same weight of large kernels ($F = 4.11$; df = 1,8; P=0.0772). The numbers of beetles emerging from small kernels was 266.8 ± 17.8 while the number emerging

from large kernels was only 219.9 ± 17.3. Laboratory analysis of these kernels indicated that the average weight of small kernels was 23.31 ± 0.22 mg while larger kernels had a mean weight of 40.76 ± 0.27 mg.

Discussion

Significant differences in total number of progeny in Experiment 1 vs. Experiments 2 and 3 were likely due to environmental factors. Experiment 1 was conducted during the fall season of the year while Experiments 2 and 3 were conducted during the winter and spring, respectively. Even though this is a laboratory colony of insects, they may still exhibit some intrinsic characteristics of wild populations such as variation in reproduction across seasons.

This study consistently showed that temperature, at least between 27.0° and 34.0° C, does not affect numbers of lesser grain borer progeny when incubated for the same number of degree days. It could be assumed that at elevated temperatures, the incidence of mortality would be higher and the overall number of adult progeny would be lower. It is important that these observations were calculated in degree days. There was an obvious difference in rate of development between the two temperatures, with beetles reared at 34.0° emerging before those reared at 27.0° C.

This study clearly showed that cultivars of wheat vary significantly in their susceptibility to infestation by lesser grain borers. In all three experiments 'Newana', 'Madison', and 'Wawawai' were grouped similarly among the most resistant cultivars. No single cultivar demonstrated complete resistance to lesser grain borer. 'Coker 916' and 'Monroe' consistently harbored large numbers of progeny while progeny numbers

harbored from 'Triumph 64' were inconsistent. While new wheat cultivars are bred for resistance to insects and disease problems in field settings, very limited consideration has been given to postharvest insect issues. As evidenced by the wide gradient of susceptibility among cultivars in this research, cultivars can have a significant influence on the apparent resistance or lack thereof to lesser grain borer (Bhatia and Gupta 1969).

Experiment 1 and the kernel size experiment revealed that physical kernel size was responsible for limiting progeny numbers. Kernel size is a result of positioning of the kernel on plant while still in the field (Kirby 1974, Simmons & Moss 1978); however, chemical composition within kernels of the same cultivar is similar. If each kernel represents an ovipositional or larval infestation site, then fewer eggs may be laid in collections of large kernels because fewer ovipositional sites are available in the same jar. Crombie (1944) documented intraspecific competition, resulting in mortality of one individual, between lesser grain borers when tunneling in the same kernel. Since there are fewer kernels the same weight of a large kernel cultivar there are potentially fewer total sites for larval development.

In Experiments 2 and 3, physical kernel size did not relate well with quantity of progeny. Possibly, the low numbers of progeny harbored in Experiments 2 and 3 contributed to the lack of significant relationship with kernel characteristics because there were less opportunities for significant differences. Previously, Amos et al. (1986) found that grain weight was a significant factor in reproduction by *R. dominica;* however McGaughey et al. (1990) found the contrary. The inconsistency noticed among experiments in this project could be responsible for conflicting conclusions in the literature.

Hardness is a widely measured parameter of kernels that is also related to different functional properties of each wheat class (Pomeranz et al. 1988). In this study, hardness did not correlate well with reproduction of lesser grain borers. These findings support the conclusions of numerous other authors (Bhatia and Gupta 1969, Amos et al. 1986, Sinha et al. 1988, McGaughey et al. 1990). It is known that hardness can strongly influence the ability of other stored product insects, such as rice weevils, to reproduce in stored wheat (McGaughey et al. 1990). Hardness did not influence progeny production by lesser grain borers in this research.

Amos et al. (1986) found protein content helped to predict quantity of progeny by lesser grain borers. None of these three experiments support this hypothesis. In addition, none of the other individual kernel parameters measured correlated with quantity of progeny production. Since testing of physical characteristics and protein content did not relate to progeny potential, other factors need to be evaluated. A good starting places for such research might include other nutrients and allelochemicals.

Biochemical resistance to lesser grain borer could possibly be bred into wheat cultivars. Cinco et al. (1991) were successful at demonstrating that water extracts of resistant wheat cultivars inhibited the amylase activity of lesser grain borers *in vitro*. Molecular genetic techniques have proven successful for other pest species in postharvest storage. Pueyo et al. (1995) demonstrated the ability of proteinaceous inhibitors from *Phaseolus vulgaris* L. (Leguminosae) to be effective *in vitro* against α-amylase of the red four beetle, *Tribolium castaneum* (Herbst). They also demonstrated the technique by adding 1% of the inhibitors to a diet consisting of wheat flour plus germ and slowed the

development of *T. castaneum* larvae. Zhu et al. (1996) demonstrated a gene specific to *N-acetylglucosamine* from *Griffonia simplicifolia* (Leguminosae) had insecticidal properties to the cowpea weevil, *Callosobruchus maculatus* (F.). However, more work on factors that contribute to quantity of lesser grain borer progeny needs to be completed before undertaking breeding projects.

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Table 1. Mean ± (standard deviation) physical and chemical parameters of each wheat cultivar.

	Cultivar			
Parameter[a]	'2180'	'Newana'	'Monroe'	'Munich'
NIR Hardness[b]	130.8	101.9	140.1	179.8
SK Hardness[c]	79.5 (30.6)	58.6 (14.0)	94.4 (17.0)	93.6 (13.2)
Percent Protein	11.8	11.5	15.0	14.9
Avg. Weight[d]	30.6 (6.5)	36.6 (7.7)	36.3 (12.8)	39.4 (11.0)
Avg. Peak Force[e]	997.7 (307.4)	1070.1 (319.7)	1516.0 (594.9)	1629.1 (507.4)
Avg. Conductance[f]	1224.3 (146.6)	1605.6 (136.1)	985.2 (212.3)	1082.6 (163.2)
Avg. Area[g]	230,588.6 (74,000)	269,259.9 (85,500)	316,555.7 (150,000)	3339,830.1 (125,000)
Avg Length[h]	383.9 (40.3)	417.2 (43.9)	404.5 (58.5)	417.0 (49.3)
Avg. Diameter[i]	2.2 (0.4)	2.5 (0.4)	2.4 (0.6)	2.5 (0.5)

Table 1. Continued.

Parameter[a]	Cultivar			
	'Triumph 64'	'Coker 916'	'Madison'	'Wawawai'
NIR Hardness[b]	75.3	26.3	41.0	42.0
SK Hardness[c]	66.0 (16.6)	7.2 (13.4)	10.3 (14.7)	26.0 (15.0)
Percent Protein	16.7	10.6	12.9	11.1
Avg. Weight[d]	21.2 (5.5)	29.3 (6.4)	33.5 (7.9)	42.2 (11.5)
Avg. Peak Force[e]	590.8 (198.1)	482.5 (146.7)	564.0 (196.3)	919.8 (328.5)
Avg. Conductance[f]	1751.6 (184.6)	1846.5 (146.5)	1630.5 (164.2)	1409.4 (191.7)
Avg. Area[g]	122,356.2 (42,800)	118,231.9 (36,100)	144,920.3 (48,600)	242,000.0 (96,600)
Avg Length[h]	341.0 (36.3)	375.1 (39.4)	389.6 (40.8)	417.5 (52.4)
Avg. Diameter[i]	1.8 (0.3)	2.1 (0.4)	2.3 (0.4)	2.5 (0.5)

[a]n for each cultivar = 300 kernels, except NIR is based on a ≈ 4 g sample and protein is based on 1 g sample. [b]Near-Infrared Reflectance, a relative measure of hardness, machine does not provide standard deviation. [c]Single Kernel Hardness, unitless. [d]Kernel

weight in mg. [e]Average peak force required to crush each kernel, unitless. [f]Conductance of each kernel, unitless. [g]Average area under the load profile, unitless. [h]Length of time required to complete crush of each kernel, unitless. [i]Average diameter of each kernel in mm.

Table 2. Mean ± SE lesser grain borer progeny per cultivar during Experiment 1.

Cultivar	Mean Number of Beetles	SE
'Triumph 64'	939.7a	134.2
'Coker 916'	866.3a	77.1
'Monroe'	700.8ab	76.9
'Munich'	645.3b	104.5
'2180'	624.3b	84.5
'Madison'	570.0b	69.9
'Newana'	569.6b	53.4
'Wawawai'	568.0b	66.8

n = 16; $F = 3.01$; df = 7, 98; $P = 0.0066$. Means followed by the same letter are not significantly different ($P>0.05$; LSD test).

Table 3. Linear regression analyses between mean physical and chemical wheat cultivar parameters and mean lesser grain borer progeny during Experiment 1.

Parameter[a]	R^2	*F*	*P*	Slope ± (SE)	Y-intercept ± (SE)
NIR Hardness	0.0541	0.343	0.5795	-0.0108 (0.0184)	26.2754 (1.9411)
SK Hardness	0.0024	0.014	0.9088	-0.0035 (0.0292)	25.4734 (1.8617)
Percent Protein	0.1309	0.903	0.3786	0.4113 (0.4327)	19.9274 (5.7086)
Avg. Weight	0.6091	9.348	0.0223	-0.3016 (0.0986)	35.4256 (3.374)
Avg. Peak Force	0.1567	1.115	0.3317	-0.0023 (0.0022)	27.5700 (2.3430)
Avg. Conductance	0.1995	1.495	0.2673	0.0036 (0.0029)	20.1110 (4.3197)
Avg. Area	0.3024	2.601	0.1579	0.0000 (0.0000)	28.9121 (2.3927)
Avg. Length	0.6311	10.265	0.0185	-0.0758 (0.0237)	55.0905 (9.3217)
Avg. Diameter	0.6234	90931	0.0198	-7.8309 (2.4850)	43.3180 (5.7541)

[a]Parameter designations are as in Table 1. For each regression df = 1, 6; n =1.

Table 4. Mean ± SE lesser grain borer progeny per cultivar during Experiment 2.

Cultivar	Mean Number of Beetles	SE
'Coker 916'	349.1a	46.2
'Monroe'	312.1ab	26.0
'Munich'	284.6abc	50.3
'2180'	277.6bc	56.1
'Wawawai'	231.6cd	29.9
'Triumph 64'	218.9cd	32.2
'Madison'	176.3d	21.1
'Newana'	122.8e	23.5

n = 16; $F = 11.79$; df = 7, 98; $P = 0.0001$. Means followed by the same letter are not significantly different ($P>0.05$; LSD test).

Table 5. Linear regression analyses between mean physical and chemical wheat cultivar parameters and mean lesser grain borer progeny during Experiment 2.

Parameter[a]	R^2	*F*	*P*	Slope ± (SE)	Y-intercept ± (SE)
NIR	0.0181	0.113	0.7486	0.0061 (0.0183)	14.4757 (1.9298)
SKH	0.0170	0.104	0.7582	0.0091 (0.0283)	14.5453 (1.8035)
KJPROT	0.0048	0.029	0.8702	0.0770 (0.4519)	14.0370 (5.96165)
AVGWT	0.0048	0.029	0.8712	-0.0260 (0.1530)	15.9150 (5.2519)
AVGPK	0.0298	0.184	0.6827	0.0010 (0.0023)	14.0676 (2.4527)
AVGC	0.1082	0.728	0.4263	-0.0026 (0.0030)	18.7589 (4.4996)
AVGAREA	0.0022	0.013	0.9115	0.000001 (0.00001)	14.7364 (2.7927)
AVGLEN	0.0242	0.149	0.7128	-0.0145 (0.03756)	20.7415 (14.7905)
AVGDIA	0.0242	0.149	0.7129	-1.5065 (3.9036)	18.5101 (9.0388)

[a]Parameter designations are as in Table 1. df for each regression = 1, 6; n = 1.

Table 6. Mean ± SE dried weights of 20 beetles per cultivar during Experiment 2.

Cultivar	Mean weight in mg	SE
'Newana'	7.964	0.171
'Monroe'	7.976	0.111
'Triumph 64'	8.030	0.1715
'Madison'	8.366	0.123
'2180'	8.447	0.206
'Munich'	8.464	0.117
'Wawawai'	8.481	0.170
'Coker 916'	8.494	0.197

n = 16; $F = 0.96$; df = 7,84; $P = 0.4629$.

Table 7. Mean ± SE lesser grain borer progeny per cultivar during Experiment 3.

Cultivar	Mean Number of Beetles	SE
'Munich'	370.1a	57.2
'Monroe'	368.3a	54.9
'Coker 916'	356.9a	45.2
'Triumph 64'	328.1ab	51.0
'2180'	290.6ab	32.2
'Wawawai'	284.0ab	38.9
'Madison'	239.9bc	33.4
'Newana'	214.3c	46.3

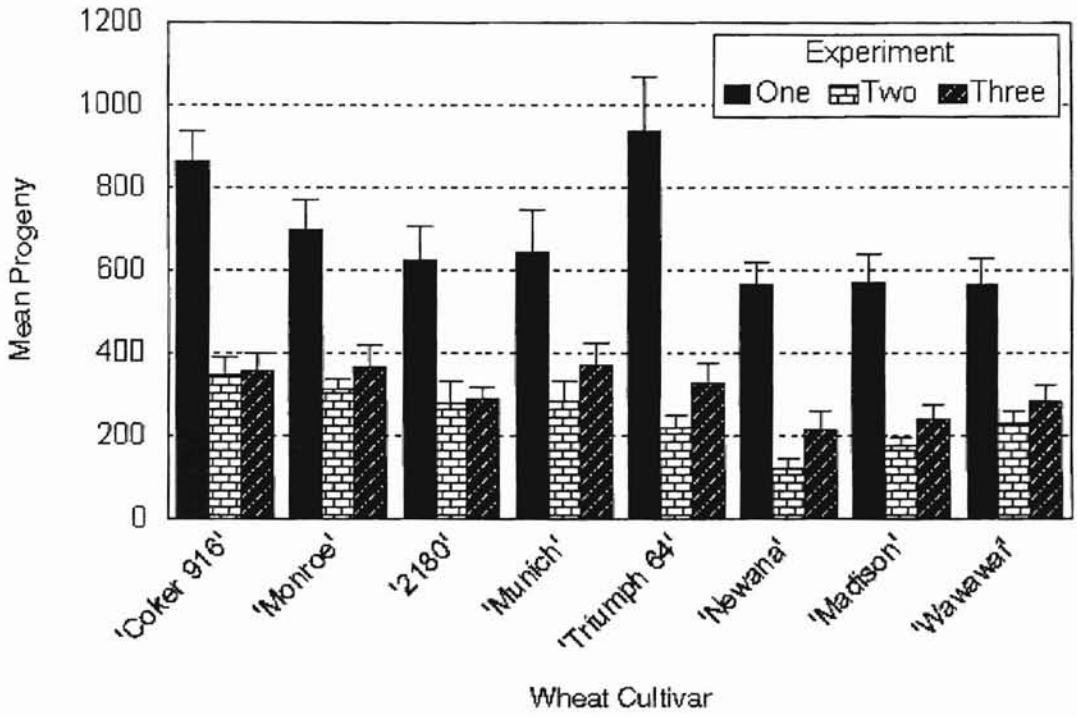
n = 16; $F = 4.19$; df = 7, 98; $P = 0.0004$. Means followed by the same letter are not significantly different ($P>0.05$; LSD test).

Table 8. Linear regression analyses between mean physical and chemical wheat cultivar parameters and mean lesser grain borer progeny during Experiment 3.

Parameter[a]	R^2	*F*	*P*	Slope ± (SE)	Y-intercept ± (SE)
NIR	0.0833	0.545	0.4882	0.0095 (0.0129)	15.9026 (1.3593)
SKH	0.1017	0.679	0.4414	0.0162 (0.0197)	15.8956 (1.2567)
KJPROT	0.1562	1.111	0.3325	0.3196 (0.3032)	12.6153 (4.0012)
AVGWT	0.0270	0.167	0.6972	-0.0452 (0.1107)	18.2981 (3.7849)
AVGPK	0.0745	0.483	0.5131	0.0012 (0.0017)	15.6568 (1.7461)
AVGC	0.1192	0.812	0.4023	-0.0020 (0.0022)	19.6224 (3.2232)
AVGAREA	0.0105	0.064	0.8093	0.000006 (0.00000)	16.2975 (2.0270)
AVGLEN	0.0603	0.385	0.5577	-0.0167 (0.0269)	23.3330 (10.5836)
AVGDIA	0.0578	0.368	0.5662	-1.6964 (2.7958)	20.6848 (6.4738)

[a]Parameter designations are as in Table 1. For each regression df = 1, 6; n = 1.

Fig. 1. Mean ± SE lesser grain borer progeny from eight different wheat cultivars during Experiments 1, 2, and 3.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'Monroe'
'2180'
'Munich'
'Triumph 64'
'Newana'
'Madison'
'Wawawai'
Wheat Cultivar

CHAPTER 3

EFFECTS OF DIVERGENT WHEAT CULTIVARS AND TEMPERATURE ON SUPPRESSION OF *RHYZOPERTHA DOMINICA* (COLEOPTERA: BOSTRICHIDAE) BY THE PARASITOID *THEOCOLAX ELEGANS* (HYMENOPTERA: PTEROMALIDAE)

Abstract

A laboratory study was conducted to examine the role of two temperatures, five divergent wheat cultivars, and the biological control agent *Theocolax elegans* on the emergence of lesser grain borer progeny. Glass jars, each with 75 g of wheat of a given cultivar, were infested with lesser grain borers and held in environmental chambers at the desired temperatures. Adult *T. elegans* were introduced into half of the jars and their progeny allowed to develop and emerge. Adult progeny of pest and parasitoid were then collected and analyzed to access efficacy of the parasitoid at suppressing its' host at the different temperatures and in the different cultivars of wheat.

Two separate trials provided different scenarios. When *R. dominica* reproduced at lower densities the parasitoid suppressed the host equally well at both temperatures. However, when the pest reproduced at greater densities, lower temperatures significantly increased the suppression of the pest population compared to that at the higher temperature. More parasitoids always emerged at lower temperatures. Analysis of interactions among the three trophic levels indicated that wheat cultivar, the first trophic level, did not significantly enhance the reproductive capacity of the third trophic level, the parasitoid. However, wheat cultivar did increase the percent suppression of the pest. This study indicates that the effectiveness of this parasitoid, and overall protection of grain, would be enhanced by aerating grain to a lower temperature.

Introduction

Biological control is an important part of integrated pest management (IPM) methods for stored grain. Parasitoids and predators occur naturally in bulk stored grain facilities (Nilakhe & Parker 1990, Vela de Garza 1993, Gates 1995) and are known to attack most insect pests of stored grain (Hagstrum & Flinn 1992). In 1992 the U.S. Food and Drug Administration (Anonymous 1992) exempted beneficial insects from tolerance standards in stored grains. This has significantly increased interest in using entomophagous insects, such as the parasitoid *Theocolax elegans* (Westwood) (Hymenoptera: Pteromalidae), in managing pests such as the lesser grain borer, *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae).

The lesser grain borer is one of the most damaging and abundant pests of stored grain in the southern United States (Cuperus et al. 1986, Vela-Coiffier et al. 1997). This insect feeds in grain both as a larva and as an adult. Detection of the species is difficult because larvae and adults tend to remain hidden inside the kernel (Fargo et al. 1989, Vela-Coiffier et al. 1997). Females feed extensively and then lay eggs singly or in small clusters exterior to the kernels (Golebiowska 1969). The first instar then bores into the kernel where it continues feeding on the endosperm, molting 3-5 times before pupation. The complete life cycle takes approximately 25 days at 34.0° C (Birch & Snowball 1945, Howe 1950). Optimal developmental temperatures for this species are 32.0° to 35.0° C (White 1995) but development can be slowed by cooling the ambient temperature of the grain (Howe 1950).

Theocolax. elegans is a solitary ectoparasitoid that parasitizes beetle larvae within the kernel. Sharifi (1972) provided an extensive list of possible hosts of *T. elegans*. Potential sites for oviposition are determined through mechanical detection using the antennae (Van Den Assem & Kuenen 1958). During oviposition the female inserts an egg into the kernel placing it on the exterior body surface of the host larva. The larva of the parasitoid continues to develop exterior to the pest larva while both are still confined within the kernel. *T. elegans* can complete one generation in approximately 25 days at 25.0° C (Van Den Assem and Kuenen 1958). The developmental time for *T. elegans* is approximately one-half that of its hosts. After emergence, the adult parasitoid bores out of the kernel.

Few studies have been conducted with augmentation of *T. elegans* populations to parasitize the lesser grain borer. Flinn et al. (1996) conducted experiments in steel grain bins in which this species was able to suppress lesser grain borer populations in excess of 90% for two years compared to the unparasitized group. In addition, lesser grain borer populations were well below the Federal Grain Inspection Service (FGIS) standard of two live insects per kg for the "sample" grade designation. Flinn (1998) also demonstrated that augmentative releases of *T. elegans* were more efficacious when coupled with lower temperatures.

One of the most effective elements of pest management in stored grain is the use of aeration to reduce temperature and/or moisture content of the grain. Aeration is accomplished by forcing cool air through a grain mass using electric fans, thus lowering the temperature of the grain. This reduction in temperature can directly affect the ability

of grain borers to reproduce in the grain mass (Cuperus et al. 1986, Kenkel et al. 1994). In contrast to chemical control, aeration is compatible with, and can actually compliment biological control by parasitoids. Utilizing this principle, a model was developed for the parasitoid *Cephalonomia waterstoni* Gahan (Hymenoptera: Bethylidae) attacking rusty grain beetle, *Cryptolestes ferrugineus* (Stephens) (Coleoptera: Cucujidae) (Flinn 1991). In Flinn's study the attack rate of the parasitoid was over two and one-half times greater at 25.0° C than at 38.0° C. When pest reproduction is slowed and parasitization increases, the number of pest insects emerging is greatly decreased compared to using either aeration or biological control independently.

Plants exhibit resistance to herbivores through antibiosis, tolerance, and antixenosis (Painter 1951, Kogan & Ortman 1978). Antibiosis refers to adverse effects by plants on the growth and development of herbivores, while tolerance relates to the ability of plants to withstand feeding. Antixenosis refers to qualities that make plants less well suited for use by herbivores, causing them to avoid those plants. Numerous scientists have conducted postharvest resistance studies showing that some wheat cultivars exhibit resistance to lesser grain borers (Bhatia & Gupta 1969, Singh & Mathew 1973, Phadke & Bhatia 1975, Amos et al. 1986, Sinha et al. 1988, McGaughey et al. 1990, Cortez-Rocha et al. 1993). Some research, although not in stored products, has shown that cultivars exhibiting antibiosis to herbivores appeared to have detrimental effects on carnivores such as parasitoids at the third trophic level (Reed et al. 1991, 1992, 1993). In comparison, plants with tolerance to herbivores appeared not to have deleterious affects at the third trophic level (Reed et al. 1993).

Ecologists use the term trophic or feeding level to delineate an organism's place in the food chain (Lindeman 1942). The management system of concern in this paper includes the wheat cultivar as the first trophic level, lesser grain borer as the second, and finally *T. elegans* as the third trophic level. Interactions among these three trophic levels are collectively termed 'tritrophic interactions.' An important consideration among tritrophic interactions is that members of the first and third trophic levels may act in a mutualistic manner (Price 1986). Starks et al. (1972) studied relationships in a cereal field crop ecosystem and quantified important observations pertinent to other ecosystems. Of primary concern in their study and several others was the concept that the primary trophic level, i.e. the host plant of the herbivore, could influence development and survivorship of a carnivorous species at the third trophic level (Starks et al. 1972, Reed et al. 1991, 1992, 1993, Reitz & Trumble 1996). A second important aspect of these studies was that activity of parasitoids at the third trophic level can influence the extent of feeding damage to the plant species. Finally, biological control and host plant resistance can be highly compatible in the development of successful pest management programs (Salto et al. 1982).

In the southern U.S., temperature in grain storage facilities are often unregulated unless aeration is employed to cool the grain as part of an IPM program. Both temperature and grain moisture contribute to the intrinsic rate of increase of lesser grain borers in stored wheat (Birch 1945a, 1945b). When aeration is used to cool grain it slows development of pest insects inhabiting the grain. However, grain cooled to temperatures in the range of 20.0° to 29.0° C is better suited for parasitoid species. Flinn (1998)

demonstrated that suppression of lesser grain borer populations by *T. elegans* was significantly better at 25.0° C than at 32.0° C.

Objectives of this study were to (1) evaluate the effects of wheat cultivar, temperature, and the parasitoid *T. elegans,* on number of lesser grain borer progeny, (2) examine interactions among the three trophic levels, (3) determine percent suppression of lesser grain borer progeny adults due to temperature and cultivar, (4) compare the ability of the parasitoid to complete its life cycle under the influence of the different temperatures, and (5) elucidate whether single kernel characteristics can be used to relate potential efficacy of T. elegans at suppressing lesser grain borer progeny.

Materials and Methods

Five cultivars of wheat were procured from commercial seed producers and various foundation seed stocks across the United States. Cultivars represented divergent genetic lineage and resistance. Wheats included the hard red winter cultivar '2163' (Oklahoma Foundation Seed Stocks, Inc., Stillwater), soft red wheats 'Coker 916' (Novartis Seeds, Inc., Bay, Arkansas) and 'Wakefield' (Arkansas Agricultural Experiment Station, Fayetteville), the durum wheat 'Munich' (North Dakota Seedstocks Project, Fargo) and a white spring wheat, 'Wawawai' (Washington State Crop Improvement Association, Pullman). Following receipt cultivars were frozen for one week to eliminate the possibility of existing infestations. Grain was then cleaned by multiple passages over a seed cleaner (Clipper model M2B, Bluffton Agricultural Industrial Corp., Bluffton, Indiana) and then tempered to 13 ± 0.5% moisture by either adding water or ambient drying. Whole wheat flour was added to each sample of wheat at a rate of one percent by

weight to stimulate oviposition by lesser grain borers. Wheat moisture contents were determined using the ASAE standard dry weight method (Society of Agricultural Engineers 1996).

Before starting the experiment, subsamples of each cultivar were analyzed at the Oklahoma State University Wheat Quality Laboratory (303 Agriculture Hall, Stillwater, OK 74078) for physical and chemical properties. Percentage protein content by weight was determined using the Kjeldahl method (American Association of Cereal Chemists 1983). Hardness measures were determined using both an NIR machine (Technicon InfraAlyzer model 400, Bran + Luebbe GmbH. Norderstedt, Germany) and a single kernel hardness (SKH) tester (Pertain Inc. Model 594. Springfield, IL). Finally, mean kernel weight, peak force required for crush, conductance, total force required for crush, time required to completely crush, and diameter were obtained using the single kernel hardness tester (Pertain Inc. Model 594. Springfield , IL). Mean values for the parameters near-infrared reflectance, single kernel hardness, peak force required for crush, conductance, area under the load profile, and length of the crush, are unitless measures intended only for comparison. Mean weight was measured in mg and mean diameter was measured in mm.

Experiments were conducted in a split plot arrangement in which the main plot was temperature, arranged in a completely randomized design, while the subplot treatments were cultivar and presence or absence of the parasitoid, arranged in a randomized complete block. Subplot treatments were blocked across the environmental chamber from left to right because an earlier uniformity trial indicated differences in the chamber. Each environmental chamber represented one application of 'temperature'

while subplot treatments were each replicated four times within each chamber. The experimental unit at the subplot level in this experiment was a jar of wheat infested with lesser grain borers. Within a subplot replication each wheat cultivar was represented two times, once in the absence of the parasitoid and once with the parasitoid present. To accommodate two subplot treatments (1. cultivar, and 2. presence or absence of the parasitoid) each replication at this level had ten jars present, five jars with parasitoids and five jars without parasitoids. Each experiment included two replications of temperature (two chambers at each experimental temperature), eight replications of cultivar with parasitoids at each temperature, and eight replications of cultivar without parasitoids (four replications within each of two chambers per temperature). The entire experiment was conducted twice.

Experiments were conducted with 75.0 ± 1.0 g of wheat in 0.2366 liter round glass canning jars. Forty, 2-3 week old unsexed lesser grain borers, from OSU stock cultures reared on hard red winter cultivar '2163', were added to each jar for a four day ovipositional period. All jars were kept at 30.0 ± 0.5° in the same chamber during the initial ovipositional period in order to begin with an equal number of eggs in each jar during each experiment. Following the ovipositional period, grain was gently sieved over a 1.40 mm standard dockage sieve. Beetles were collected below that sieve on a 0.21082 mm sieve while the dust fell through both sieves to be collected in a bottom pan. Wheat was finally returned to the jars along with the dust as eggs could be present in this fine material. Ventilation was permitted through filter paper held in place by the canning ring. Samples were maintained at either 27.0 ± 0.5° C or 34.0 ± 0.5° C and 70 ± 5% RH in

upright environmental chambers (Percival-Scientific Corp., Model I-35 LVL). Completely dark conditions were utilized throughout the experiment. During each experiment, hygrothermographs were maintained inside each environmental chamber to monitor any changes in temperature or humidity.

Time of host and parasitoid introduction and removal times are summarized in Table 1. All adult *T. elegans* had been emerged for less than three days after rearing in stock colonies on lesser grain borers in '2163' wheat. Five male and 10 female parasitoids were released at each release time. Previous research (Toews, unpublished) indicated that generation time for lesser grain borers varied among wheat cultivars. Due to the possibility of a single parasitoid release being optimally timed for a given cultivar containing the appropriate host stage, two parasitoid releases were utilized. This method insured that live parasitoids were present when their hosts reached the optimum age for parasitism. Differences in lesser grain borer developmental times at the two different experimental temperatures were estimated with a degree day model developed by Subramanyam et al. (1990). The model used a threshold temperature of 13.2° C for egg to adult development of lesser grain borers. All insect introduction and removal times of insects were calculated to occur at the same degree day intervals in both temperature treatments. Data analysis was performed only on the total number of progeny collected and not broken down by individual collection interval.

Data were analyzed using SAS (SAS Institute Inc. 1994). Before statistical analysis progeny counts were transformed using a square root transformation while percentages were transformed using the arcsine transformation (Zar 1984) to correct for

heteroscedastic data. Treatment means were compared at the α=0.05 level using the LSD method (PROC GLM, MEANS LSD LINES) (Steel & Torrie 1980). Linear regressions of progeny numbers on kernel parameters were made for data without interactions using PROC REG (SAS Institute Inc. 1994). To relate numbers of parasitoids emerged to cultivar effects, a 'parasitoid progeny production index' was created. This index was determined by dividing the total number of parasitoids emerging from each treatment jar by the total number of beetles emerged from the control jar of the same cultivar in the same replication. This index was needed to fully quantify the tritrophic nature of the study. Parasitoid counts were analyzed using PROC GLM; however, this method does not account for variability at the first trophic level from a cultivar that harbors only a few beetles and consequently only a few parasitoids. When using the parasitoid production index, numbers of *T. elegans* are related to the number of emerged beetles in the wheat without parasitoids and therefore the effect of cultivar on beetle numbers is adjusted appropriately. Parasitoid production index data were analyzed using PROC GLM (SAS 1994) and were not transformed. Values for percent suppression of lesser grain borer caused by *T. elegans* were obtained by dividing the number of lesser grain borer adults from the jar with the parasitoids present by the number adults from jars without the parasitoids in the same replication. The resulting number from that calculation was then subtracted from one and multiplied by 100.

Results

Near-infrared reflectance (NIR) hardness values ranged from 19.8 in the soft red winter cultivar 'Wakefield' to 'Munich', the hardest durum entry, 'Munich', with a

hardness value of 145.4 (Table 2). Mean weight of individual kernels from a given cultivar also varied greatly. 'Coker 916' had the lightest kernels (29.6 ± 6.7 mg) compared with kernels of 'Wawawai' that weighed a mean of 50.9 ± 9.4 mg. Mean diameter of kernels varied from a minimum of 2.1 ± 0.4 mm to a maximum of 2.9 ± 0.4 mm. The percent protein ranged from 9.3% in 'Wakefield' to 13.7% in 'Munich' (Table 2).

Production of progeny by lesser grain borers differed greatly in magnitude between the two experiments (Fig. 1). In Experiment one, the number of lesser grain borers emerging in the control jars was roughly one third of that in Experiment two. These differences existed despite identical procedures, temperatures and humidities during both experiments. The difference in number of progeny of lesser grain borers also directly influenced the magnitude of *T. elegans* reproduction in experiments. With respect to these differences, all analyses of these data are reported independently for each experiment.

During Experiment 1, there were no temperature by cultivar interactions pertaining to the number of lesser grain borer progeny in wheat without the parasitoid present. Temperature did not influence the number of lesser grain borers emerged jars of wheat without parasitoids ($F = 0.19$; df = 1,2; $P = 0.7054$). However, there were differences in the number of emerged beetles from individual wheat cultivars ($F = 10.59$; df = 4, 56; $P = 0.0001$) (Table 3). Lowest progeny numbers were produced in 'Wawawai'. In contrast, 'Coker 916' and 'Wakefield' harbored over two times as many progeny.

Physical and chemical kernel parameters that significantly influenced progeny in the control (no parasitoids present in grain) jars during Experiment 1 are summarized in Table 4. These parameters are interrelated in that each describes an aspect related to overall kernel size. Mean weight is related to mean area ($F = 16.819$; df = 1, 3; $P = 0.0262$; $R^2 = 0.8486$), mean length of crush ($F = 229593.60$; df = 1, 3; $P = 0.0001$; $R^2 = 1.0$), and mean kernel diameter ($F = 29.157$; df = 1, 3; $P = 0.0125$; $R^2 = 0.9067$), through linear regression. In each case, as kernel size increased the mean numbers of lesser grain borer progeny emerging from that cultivar decreased.

During Experiment 1, the number of lesser grain borers emerged from wheat with *T. elegans* present had a marginally significant temperature by cultivar interaction ($F = 2.28$; df = 4, 56; $P = 0.0722$). Further scrutiny of this interaction indicated that when testing simple effects of cultivar while controlling for temperature (SAS, PROC GLM, LS MEANS SLICE) 'Wawawai' was contributing more variability to this interaction ($F = 11.8122$; df = 1, 56; $P = 0.0011$) than the other cultivars, which all tested nonsignificant. Furthermore, this interaction was only significant at 34.0° C temperature ($F = 8.5033$; df = 4, 56; $P = 0.0001$) when testing simple effects of temperature while controlling for cultivars (SAS, PROC GLM, LS MEANS SLICE). This indicates that the treatment combination 'Wawawai' at 34.0° C responded significantly different than the other treatment combinations. Least squares means by treatment combination were separated using the LSD method and are summarized in Table 5. Cultivar means were similar except for 'Wawawai' at 34.0° C which harbored significantly more progeny than any other treatment combination.

During Experiment 1, percent suppression of lesser grain borers in samples containing *T. elegans* compared with those without the parasitoids had a significant temperature by cultivar interaction ($F = 2.85$; df = 4, 56; $P = 0.0320$). When this interaction was scrutinized by cultivar while controlling for temperature, only 'Wawawai' significantly contributed to the interaction ($F = 15.91$; df = 1, 56; $P = 0.0002$). Likewise, when scrutinized by temperature while controlling for cultivar, only the 34.0° C temperature was significant ($F = 11.91$; df = 4, 56; $P = 0.0001$). 'Wawawai' at 34.0° C had the lowest rate of suppression of lesser grain borers when compared to all other treatment means (Table 6). This treatment combination exhibits less resistance to increases in lesser grain borer progeny than would be expected, based on the performance of the cultivar at the lower temperature. The standard error for 'Wawawai' at 34.0° C is much larger than that for other treatment combinations because there were more lesser grain borers in that treatment (grain with parasitoids) than the control (grain without parasitoids) in one of the replications.

During Experiment 1, the number of *T. elegans* progeny also had a significant temperature by cultivar interaction ($F = 3.70$; df = 4, 56; $P = 0.0097$). This interaction was significant both at 27.0° C ($F = 13.0790$; df = 4, 56; $P = 0.0001$) and at 34.0° C ($F = 3.1082$; df = 4, 56; $P = 0.0222$) when testing main effects while controlling for cultivar. *P*-values for each cultivar were significant when testing simple effects of cultivar while controlling for temperature (Table 7). Least squares means for all treatment combinations are presented in Table 8. All treatment combinations at the upper temperature resulted in fewer parasitoids than those at the lower temperature.

The parasitoid production index calculated for Experiment 1 did not indicate any temperature by cultivar interactions. In each cultivar more *T. elegans* emerged per available host at the lower temperature (index = 0.58 ± 0.38) than the upper temperature (index = 0.12 ± 0.09). The test for main plot treatment differences indicated that this difference in index values was significant ($F = 118.47$; df = 1, 2; $P = 0.0083$). Interestingly, there were no significant differences detected among cultivars for the parasitoid production index ($F = 0.76$; df = 4, 76; $P = .5551$) (Table 9). None of the kernel parameters measured correlated with the mean index value.

Experiment 2 was different from Experiment 1in that there were major differences in the magnitude of progeny produced by lesser grain borers and *T. elegans.* In addition, there were no significant temperature by cultivar interactions. In the absence of significant interactions valid tests for significant effects of individual treatments could be conducted.

During Experiment 2, temperature was not a contributing factor to variability in number of lesser grain borer progeny ($F = 0.24$; df = 1,2; $P = 0.6733$). At 27.0° C, a mean of 358.7 ± 29.6 beetles emerged, while at 34.0° C, 398.1 ± 26.6 beetles emerged per jar of wheat. Numbers of lesser grain borer progeny in the control jars (grain without *T. elegans*) significantly varied with cultivars (F =6.52; df = 4,56; $P = 0.0002$) (Table 10). Total numbers of progeny by cultivar ranged from 248.9 ± 27.5 beetles to 487.4 ± 51.4 beetles per jar. The cultivars 'Wawawai' and 'Munich' showed much more resistance than the remaining cultivars. Mean physical and chemical parameters of kernels found to correlate with number of progeny using linear regression in the wheat

without *T. elegans* are summarized in Table 11. Cultivars with smaller kernels harbored more progeny than equal quantities, by weight, of cultivars with larger kernels. All other kernel characteristics did not significantly correlate with quantity of lesser grain borer progeny.

During Experiment 2, temperature was marginally important in influencing the number of beetles that emerged from wheat with the parasitoids present ($F = 10.88$; df = 1,2; $P = 0.0809$). At 34.0° C over three times as many beetles emerged in comparison with 27.0° C (189.9 ± 24.0 beetles at 34.0° C, 55.2 ± 9.2 beetles at 27.0° C). The wheat cultivars did not significantly influence numbers of lesser grain borer recovered from samples with the parasitoids present ($F = 0.66$; df = 4, 56; $P = 0.6217$). Progeny per cultivar ranged from 107.6 ± 18.6 to 155.8 ± 42.9 beetles per jar (Table 12). None of the regressions of kernel parameters and numbers of progeny were significant for treatments with the parasitoids present.

The higher temperature had a significant influence on the suppression of lesser grain borers when compared with the lower temperature ($F = 17.78$; df = 1,2; $P = 0.0519$). At 27.0° C the number of lesser grain borers suppressed was 81.5 ± 3.1% were as 51.3 ± 5.7% were suppressed at the higher temperature. There were no differences in percent suppression of lesser grain borer progeny attributable to the different cultivars ($F = 1.72$; df = 4, 55; $P = 0.1580$) (Table 13). Suppression of lesser grain borers ranged from a minimum of 56.9 ± 8.2% in 'Wawawai' to a high of 73.3 ± 8.5% in '2163'. Kernel parameters found to relate with percent suppression of lesser grain borers by *T.*

elegans through linear regression are presented in Table 14. Again, as the kernel size increased the percent suppression of lesser grain borers decreased.

During Experiment 2, temperature played an important role in recovery of adult parasitoid progeny ($F = 9.94$; df = 1, 2; $P = 0.0876$). While a mean of only 24.2 ± 5.3 *T. elegans* emerged from wheat samples held at 34.0° C, a mean of 206.5 ± 16.0 parasitoids emerged from grain held at 27.0° C. Fewer *T. elegans* progeny emerged from 'Wawawai' than from the remaining cultivars (Table 15). This was expected since this cultivar also harbored the fewest number of lesser grain borers. Kernel parameters with a significant regression with adult parasitoid progeny included mean kernel weight, length of crush, and diameter (Table 16). Fewer parasitoids emerged from cultivars with larger kernels. This may be due to increased host availability in cultivars with smaller kernels.

During Experiment 2 the parasitoid progeny production index was significantly higher at 27.0° C than at 34.0° C ($F = 19.93$; df = 1, 2; $P = 0.0467$). At the higher temperature the mean parasitoid production index was only 0.11 ± 0.03 while at 27.0° C it was 0.69 ± 0.09. The index was not influenced significantly by wheat cultivar ($F = 1.80$; df = 4, 56; $P = 0.1416$) (Table 17). Values for the index ranged from a minimum of 0.27 ± 0.07 parasitoids per available host in 'Wawawai' to a maximum of 0.58 ± 0.20 parasitoids per available host in 'Munich'. None of the kernel parameters were significant in linear regression with the parasitoid production index.

Discussion

The reasons for magnitude difference in the number of progeny of lesser grain borers between the two Experiments were probably due to one or more environmental

and seasonal differences. Experiment 1 was conducted during the spring of the year, while Experiment 2 was conducted during the summer. Even though this is a laboratory colony of insects, they may still exhibit some characteristics of wild populations such as variation in reproduction across seasons.

Fewer adult beetle progeny were recovered, in the wheat without parasitoids, in the cultivars with larger kernels. Kernel parameters found to relate with increased quantity of recovered lesser grain borers were all related to kernel size. It is unclear why larger kernel size resulted in fewer progeny. Theoretically, if each kernel represents an ovipositional site, then fewer eggs are laid on large kernels due to fewer available ovipositional sites in the same quantity of grain by weight. Intraspecific competition by larvae within the same tunnel has been documented for lesser grain borers (Crombie 1944); in this case the larger larva would kill the smaller one. The increase in kernels per unit area in a cultivar with smaller kernels could decrease the chances of two larvae inhabiting the same kernel.

The regression analyses showed that parameters including mean kernel weight, area under the crush profile, length of time needed to crush, and kernel diameter all were significant in the regressions with percent suppression of lesser grain borer progeny. These results suggest that smaller kernels promote parasitism of lesser grain borers *by T. elegans*. It is possible that female parasitoids have more difficulty finding hosts in cultivars with larger kernels. Large kernels may have a greater distance between the exterior surface, where the parasitoid contacts the grain, and the location of the host within the kernel. This increase could make it difficult for parasitoids to find hosts since *T. elegans* is known to locate hosts by drumming the antennae on the kernel (Van den

Assem & Kuenen 1958). When a female parasitoid is searching for hosts a reduction in the intensity of stimulation to the antennae would require more handling time per host. Another possibility is that *T. elegan's* ovipositor may not reach host larvae deep within large kernels, as first postulated by Williams and Floyd (1971).

During Experiment 1, the percent suppression in progeny production of lesser grain borers was similar between temperatures suggesting that the same proportion of hosts appear to have been stung in each case. However, during Experiment 2 the percent suppression decreased significantly at 34.0° C, strongly suggesting that fewer hosts were stung at higher temperature. This discrepancy is likely due to differences in host density between the experiments and can be explained as a change in the functional response of the parasitoid at different temperatures.

The functional response is the change in the number of hosts consumed or parasitize (stung) by individual predators or parasitoids as the density of the prey/host changes (Solomon 1949, Holling 1959). Later, Mack & Smilowitz (1982) suggested that search rate, a component of the functional response, decreased in relation to increasing temperatures above 30.0 C for the predator *Coleomegilla maculata* (DeGeer). (Coleoptera: Coccinellidae). Likewise, Flinn (1991) described and modeled the functional response of a stored grain parasitoid, *Cephalonomia waterstoni* (Gahan) (Hymenoptera: Bethylidae). He found that both searching rate and handling time of the parasitoid were decreased by high ambient temperatures in the wheat.

The functional response concept is a useful tool to help explain differences in beetle suppression between these experiments. Here the functional response describes the

number of hosts stung by the parasitoid. While the total number of parasitoids released into each experiment was constant, the host density between experiments was quite different. During Experiment one, the search and handling time of the parasitoid could have increased at the upper temperature but the suppression rate would stay the same if there were enough time and parasitoids to sting the limited number of hosts. In Experiment two the host density was much higher. An increase in the search and handling time due to the higher temperature, at this host density, could have resulted in lower suppression of the host, since there were not enough parasitoids to sting the large number of available hosts. At the lower temperature of Experiment two, the parasitoids were able to attack their hosts quicker and likely parasitized a higher proportion of the pest population. Data from Experiment 2 imply that temperature is an important component of the functional response for *T. elegans*.

In both of these experiments, the 34.0° temperature significantly limited the number of parasitoids that emerged as adults. Possibly, the high temperature prohibited a certain physiological event from occurring somewhere between oviposition and adult emergence. Another hypothesis is that hosts at the high temperature are being stung, thus paralyzing the larvae, but adult female parasitoids are not depositing eggs; this behavior has been shown with another species of stored grain parasitoid (Flinn 1991).

Solomon (1949) described the numerical response, defined as a change in the number of predators, as a function of prey density from generation to generation. Entomophagous insects in biological control studies usually control pest populations through changes in the numerical response (Huffaker et al. 1976). The current

experiments do not include conclusions on the numerical response of the parasitoid because these conclusions would require data from several generations. However, in both of these experiments, significantly more *T. elegans* emerged per available host at the lower temperature than at the higher temperature. Assuming that host density is not a limiting factor and that more parasitoids are able to parasitize an increased number of hosts, the potential for a numerical response should be increased at the 27.0° C temperature, compared to 34.0° C. Additional research targeting the numerical response for this parasitoid is needed to address these possibilities.

Cultivar played a limited role in the association among trophic levels. Differences in numbers of *T. elegans* recovered among cultivars may be linked to the increased number of lesser grain borer hosts in less resistant cultivars. The parasitoid progeny production index provides more information on the wheat cultivar's influence on the parasitoid. A higher parasitoid production index value, such as that calculated for 'Munich' during both experiments, suggested that the first trophic level is positively influencing the third trophic level. More parasitoids emerged per potential host on the cultivar 'Munich' than in 'Wawawai', however cultivar was not a statistically significant factor contributing to differences in the index value in either experiment. This study sought to identify characteristics of wheat cultivars contributing to higher parasitoid emergence index values. Unfortunately, none of the kernel parameters measured in this study correlated well with the parasitoid emergence index.

Conclusions

T. elegans played an important role in suppressing progeny production of lesser grain borer. Suppression of the second trophic level (lesser grain borer) by the third trophic level (parasitoid) will prevent excessive losses at the first trophic level (grain). There were no differences in the numbers of lesser grain borer progeny at either experimental temperature; however, high temperature significantly decreased emergence by *T. elegans.* In addition, even when suppression of the pest was similar between temperatures, more parasitoids emerged at the cooler temperature thereby potentially increasing the opportunity for successful control. Efficacy of the parasitoid at high pest density was increased by the lower temperature. The first trophic level, wheat cultivar, did not significantly effect the parasitoid production index.

Further research is needed to describe the functional and numerical responses of *T. elegans* through a range of temperatures. It is possible that this species could be even more efficient at temperatures below 27.0 C. Further research is also needed to identify characteristics of cultivars that may enhance parasitoid reproduction. This study indicated that biological control of lesser grain borer using the parasitoid *T. elegans* could be an important aspect of stored grain management.

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Table 1. Introduction and removal times for lesser grain borers and *T. elegans* during Experiments 1 and 2.

Temperature	*T. elegans* Released		*T. elegans* Released		*T. elegans* Removed		*R. dominica* and *T. elegans* removed		*R. dominica* and *T. elegans* removed	
	DD[a]	Day[b]	DD	Day	DD	Day	DD	Day	DD	Day
27.0° C	343.2	24	453.6	32	564.0	40	771.0	55	978.0	70
34.0° C	337.6	17	441.6	22	566.4	28	774.4	38	982.4	48

[a]Degree Days based on a model by Subramanyam et al. (1990). [b]Actual Calendar day of experiment starting with adult *R. dominica* release when all jars were held at 30.0° C for four days accounting for the first 67.2 degree days in this table; after the four day ovipositional period the adult *R. dominica* were removed and jars moved to their respective temperatures. If 24 actual calendar days are shown in this table then the first four days were at 30.0° C and the other 20 days are at the experimental temperature.

Table 2. Mean ± standard deviation physical and chemical parameters of kernels of each wheat cultivar.

Parameter[a]	Cultivar				
	'Wakefield'	'Coker 916'	'2163'	'Munich'	'Wawawai'
NIR Hardness[b]	19.8	24.9	104	145.4	74.9
SK Hardness[c]	1.2 (13.5)	9.1 (16.2)	80.1 (20.0)	92.9 (18.7)	32.8 (13.1)
Percent Protein[d]	9.3	10.2	11.5	13.7	10.7
Weight[e]	34.3 (7.2)	29.6 (6.7)	26.7 (6.0)	37.4 (9.8)	50.9 (9.4)
Peak Force[f]	569.6 (183.2)	470.7 (156.9)	863.9 (252.7)	1596.9 (521.2)	1276.1 (340.1)
Conductance[g]	1718.9 (130.6)	1701.3 (140.7)	1447.1 (132.7)	1235.6 (177.1)	1707.7 (141.5)
Area[h]	145461.5 (46100)	114981.1 (37400)	180835.1 (55200)	335636.1 (125000)	351971.5 (99900)
Length of Crush[i]	390.5 (43.4)	376.0 (40.3)	372.5 (36.4)	4.26.8 (51.5)	457.2 (42.0)
Diameter[j]	2.3 (0.4)	2.1 (0.4)	2.1 (0.3)	2.6 (0.5)	2.9 (0.4)

[a]n for each measurement = 300, except NIR hardness is based on a 4.0 g ground sample and percent protein is based on a 1.0 ground sample. [b]Near-Infrared Reflectance, a unitless measure of hardness, machine does not provide error term. [c]Single Kernel Hardness, a

unitless measure of hardness. [d]Percent protein as determined by the Kjeldahl method. [e]Kernel weight in mg. [f]Mean peak force required to crush each kernel, a unitless measure. [g]Conductance of each kernel. [h]Mean area under the load profile measured in time intervals. [i]Length of time required to complete crush of each kernel. [j]Mean diameter of each kernel in mm.

Table 3. Mean ± SE lesser grain borer emergence from grain, without *T. elegans* present, during Experiment 1.

Cultivar	Mean Progeny	SE
'Coker 916'	148.5a	15.7
'Wakefield'	140.5ab	20.1
'2163'	133.0ab	17.4
'Munich'	106.3b	10.6
'Wawawai'	65.6c	10.9

n = 16; $F = 10.59$; df = 4, 56; $P = 0.0001$. Means followed by the same letter within columns are not significantly different ($p>0.05$; Fishers LSD Test).

Table 4. Mean physical and chemical parameters of cultivar kernels found to relate with mean lesser grain borer emergence from wheat, without *T. elegans* present, during Experiment 1.

Parameter	R^2	*F*	*P*	Slope ± (SE)	Y-intercept ± (SE)
Weight	0.8685	19.818	0.0211	-5.2696 (1.1837)	92.7768 (12.9277)
Area	0.8191	13.586	0.0346	-60168 (16323)	876787 (178278)
Length of Crush	0.9053	28.689	0.0127	-20.8720 (3.8968)	630.4223 (42.5583)
Diameter	0.9067	29.157	0.0125	-0.2062 (0.0382)	4.6455 (0.4171)

df = 1, 3; n = 1.

Table 5. Mean ± SE lesser grain borer progeny emergence from treatment combinations in wheat, with *T. elegans* present, during Experiment 1.

Treatment Combination	Mean Progeny	SE
'Wawawai' at 34.0° C	27.5a	10.9
'Wawawai' at 27.0° C	9.1b	3.8
'Munich' at 34.0° C	9.8b	4.8
'Wakefield' at 27.0° C	8.6b	4.9
'Wakefield' at 34.0° C	6.5b	2.8
'Munich' at 27.0° C	6.0b	2.4
'Coker 916' at 34.0° C	4.1b	1.9
'Coker 916' at 27.0° C	3.9b	2.0
'2163' at 34.0° C	3.1b	1.2
'2163' at 27.0° C	3.6b	1.9

n = 8; $F = 2.28$; df = 4, 56; $P = 0.0722$. Means followed by the same letter within columns are not significantly different ($p>0.05$; Fishers LSD Test).

Table 6. Mean ± SE lesser grain borer percent suppression by treatment combination as a result of *T. elegans* during Experiment 1.

Treatment Combination	Mean % Suppression	SE
'Coker 916' at 27.0° C	97.88a	0.96
'Coker 916' at 34.0° C	97.76ab	0.95
'2163' at 27.0° C	96.68ab	1.67
'2163' at 34.0° C	96.36ab	1.63
'Wakefield' at 27.0° C	95.27ab	2.03
'Munich' at 27.0° C	94.97ab	2.09
'Wakefield at 34.0° C	94.52ab	1.58
'Munich' at 34.0° C	90.75ab	3.72
'Wawawai' at 27.0° C	87.84b	3.11
'Wawawai' at 34.0° C	44.64c	21.47

n = 8; $F = 2.85$; df = 4, 56; $P = 0.0320$. Means followed by the same letter within columns are not significantly different ($p>0.05$; Fishers LSD Test).

Table 7. *P*-values by cultivar, when controlling for temperature, for number of parasitoid progeny during Experiment 1.

Cultivar	*F*	df	*P*
'2163'	83.9573	1, 56	0.0001
'Munich'	37.3672	1, 56	0.0001
'Coker 916'	32.6349	1, 56	0.0001
'Wakefield'	53.2311	1, 56	0.0001
'Wawawai'	15.9132	1, 56	0.0002

Table 8. Mean ± SE *T. elegans* progeny from varying treatment combinations during Experiment 1.

Treatment Combination	Mean Progeny	SE
'2163' at 27.0° C	79.1a	10.0
'Wakefield' at 27.0° C	68.00ab	7.9
'Coker 916' at 27° C	64.6ab	10.8
'Munich' at 27.0° C	58.6b	14.0
'Wawawai' at 27.0° C	25.4c	6.4
'Coker 916' at 34° C	21.1cd	5.2
'Wakefield' at 34.0° C	16.3cd	5.6
'Munich' at 34.0° C	15.1cd	4.6
'2163' at 34.0° C	13.4de	5.6
'Wawawai' at 34.0° C	6.0e	1.7

n = 8; $F = 3.70$; df = 4, 56; $P = 0.0097$. Means followed by the same letter within columns are not significantly different ($p>0.05$; Fishers LSD Test).

Table 9. Mean ± SE *T. elegans* progeny production index during Experiment 1.

Cultivar	Mean Index	SE
'2163'	0.44	0.14
'Munich'	0.37	0.08
'Coker 916'	0.34	0.08
'Wakefield'	0.32	0.06
'Wawawai'	0.29	0.07

n = 16; $F = 0.76$; df = 4, 56; $P = 0.5551$.

Table 10. Mean ± SE lesser grain borer progeny from wheat, without *T. elegans* present, during Experiment 2.

Cultivar	Mean Progeny	SE
'Wakefield'	487.4a	51.4
'2163'	443.1a	41.4
'Coker 916'	377.0ab	38.0
'Munich'	335.5bc	39.2
'Wawawai'	248.9c	27.5

n = 16; $F = 6.52$; df = 4, 56; $P = 0.0002$. Means followed by the same letter within columns are not significantly different ($p>0.05$; Fishers LSD Test).

Table 11. Mean physical and chemical parameters of cultivar kernels found to relate with mean lesser grain borer progeny in wheat, without *T. elegans* present, during Experiment 2.

Parameter	R^2	*F*	*P*	Slope ± (SE)	Y-intercept ± (SE)
Weight	0.6705	6.105	0.0900	-3.1304 (1.267)	96.3056 (24.6618)
Length of Crush	0.7294	8.088	0.0654	-12.6670 (4.4541)	649.5795 (86.6984)
Diameter	0.7325	8.214	0.0643	-0.1253 (0.0437)	4.8380 (0.8512)

df = 1,3; n = 1.

Table 12. Mean ± SE lesser grain borer progeny emergence from wheat, with *T. elegans* present, during Experiment 2.

Cultivar	Mean Progeny	SE
'Wakefield'	155.75	42.9
'2163'	119.5	44.1
'Coker 916'	116.2	28.0
'Munich'	113.5	28.3
'Wawawai'	107.6	18.6

n = 16; $F = 0.66$; df = 4, 56; $P = 0.6217$.

Table 13. Mean percent ± SE suppression of lesser grain borer progeny when parasitized by *T. elegans* during Experiment 2.

Cultivar	Mean % Suppression	SE
'2163'	73.3	10.7
'Coker 916'	71.0	5.7
'Wakefield'	70.1	6.8
'Munich'	61.9	10.7
'Wawawai'	55.9	8.2

n = 16; $F = 1.72$; df = 4, 55; $P = 0.1580$.

Table 14. Mean physical and chemical parameters of cultivar kernels found to relate with mean percent suppression of lesser grain borer progeny during Experiment 2.

Parameter	R^2	*F*	*P*	Slope ± (SE)	Y-intercept ± (SE)
Weight	0.9107	30.582	0.0117	-93.6000 (16.9256)	104.0667 (12.4364)
Area	0.8292	14.569	0.0316	-1050137 (275128)	992126 (202154)
Length of Crush	0.9884	255.677	0.0005	-378.3048 (23.6590)	680.6621 (17.3838)
Diameter	0.9888	265.037	0.0005	-3.7359 (0.2295)	5.1404 (0.1686)

df = 1,3; n = 1.

Table 15. Mean ± SE *T. elegans* progeny during Experiment 2.

Cultivar	Mean Progeny	SE
'2163'	147.9a	36.3
'Munich'	127.9a	30.7
'Coker 916'	127.4a	30.3
'Wakefield'	122.2a	29.8
'Wawawai'	51.4b	13.9

n = 16; $F = 10.52$; df = 4, 56; $P = 0.0001$. Means followed by the same letter within columns are not significantly different ($p>0.05$; Fishers LSD Test).

Table 16. Mean physical and chemical parameters of cultivar kernels found to relate with mean *T. elegans* progeny during Experiment 2.

Parameter	R^2	*F*	*P*	Slope ± (SE)	Y-intercept ± (SE)
Weight	0.8943	25.370	0.0151	-4.5386 (0.9011)	83.9622 (9.6987)
Length of Crush	0.7108	7.374	0.0728	-15.6984 (5.7808)	571.3105 (62.2212)
Diameter	0.7123	7.428	0.0722	-0.1551 (0.0569)	4.0619 (0.6127)

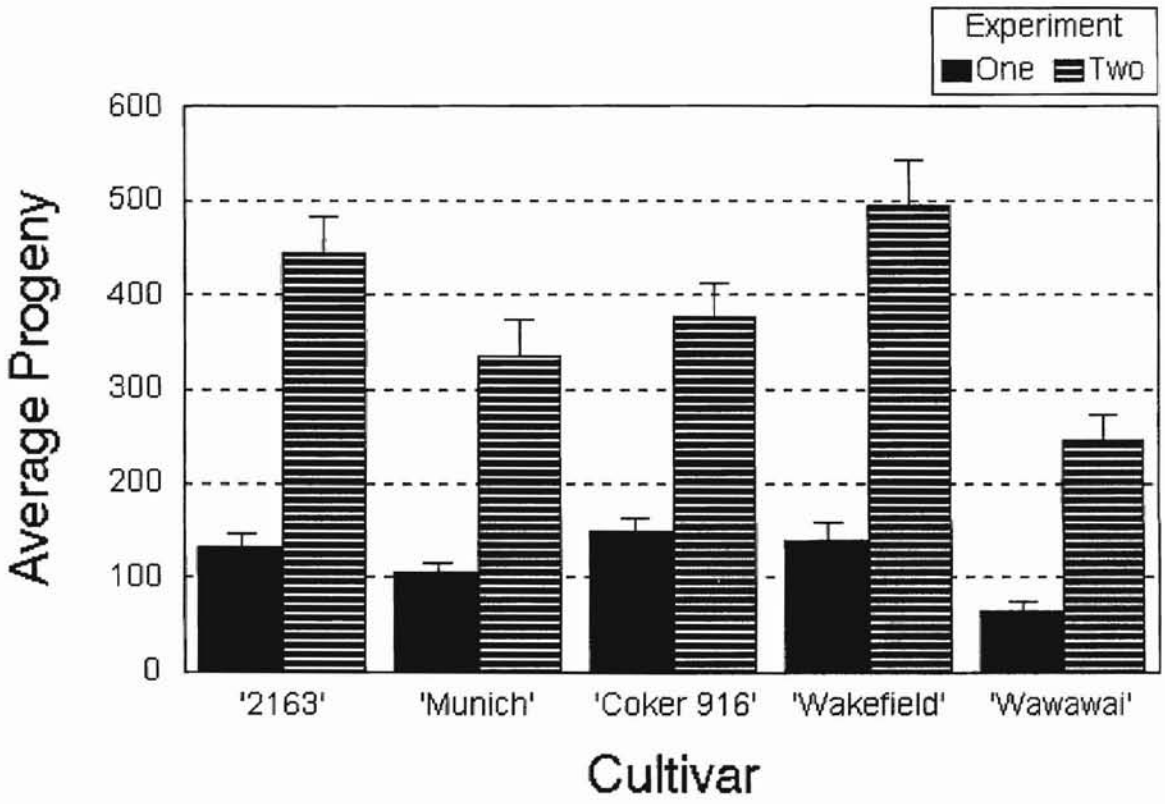
df = 1,3. n = 1.

Table 17. Mean ± SE *T. elegans* progeny production index during Experiment 2.

Cultivar	Mean Index	SE
'Munich'	0.58	0.20
'Coker 916'	0.45	0.13
'2163'	0.40	0.10
'Wakefield'	0.29	0.07
'Wawawai'	0.27	0.07

n = 16; $F = 1.80$; df = 4, 56; $P = 0.1416$.

Fig. 1. Mean ± SE lesser grain borer progeny emerging from wheat without *T. elegans* present during Experiments one and two.


Experiment
One
Two
600
500
400
300
200
100
0
Average Progeny
'2163'
'Munich'
'Coker 916'
'Wakefield'
'Wawawai'
Cultivar

VITA

Michael D. Toews

Candidate for the Degree of

Master of Science

Thesis: INFLUENCE OF WHEAT CULTIVAR, TEMPERATURE, AND *THEOCOLAX ELEGANS* (HYMENOPTERA: PTEROMALIDAE) ON *RHYZOPERTHA DOMINICA* (COLEOPTERA: BOSTRICHIDAE) DEVELOPMENT

Major Field: Entomology

Biographical:

Personal Data: Born in Salina, Kansas, on 17 November 1972, the son of Dennis and Renee Toews.

Education: Graduated from Salina South High School, Salina, Kansas in May 1991; received Bachelor of Science degree in Field Biology from Fort Hays State University, Hays, Kansas in May 1995. Completed the requirements for the Master of Science degree with a major in Entomology at Oklahoma State University in May 1998.

Experience: Worked as an Interpretive Naturalist for the Kansas Dept. of Wildlife and Parks during the summers of 1993 and 1994; worked as a crop scout for Collingwood Grain Inc. at Oakley, Kansas during the summer of 1995; employed by the Oklahoma State University as a graduate research/teaching assistant; Oklahoma State University, Department of Entomology, 1995 to present.

Professional Memberships: Entomological Society of America, Southwestern Entomological Society