Evolution of Stored-Product Entomology: Protecting the World Food Supply

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Abstract

Traditional methods of stored-product pest control were initially passed from generation to generation. Ancient literature and archaeology reveal hermetic sealing, burning sulfur, desiccant dusts, and toxic botanicals as early control methods. Whereas traditional nonchemical methods were subsequently replaced by synthetic chemicals, other traditional methods were improved and integrated with key modern pesticides. Modern stored-product integrated pest management (IPM) makes decisions using knowledge of population dynamics and threshold insect densities. IPM programs are now being fine-tuned to meet regulatory and market standards. Better sampling methods and insights from life histories and ecological studies have been used to optimize the timing of pest management. Over the past 100 years, research on stored-product insects has shifted from being largely concentrated within 10 countries to being distributed across 65 countries. Although the components of IPM programs have been well researched, more research is needed on how these components can be combined to improve effectiveness and assure the security of postharvest food as the human population increases.

INTRODUCTION

Stored-product entomology has evolved through five phases. First, traditional methods of pest control were adapted and passed from generation to generation, as agriculture evolved from individuals growing their own food to a postindustrial society in which a few farmers fed large populations and international trade began to spread insect pests throughout the world. Second, synthetic chemical controls replaced many traditional nonchemical methods and allowed for large mass storage of commodities. Pesticide regulations and resistance in pest populations led to safer and more effective integrated pest management (IPM). Third, traditional methods were improved and integrated with a few key chemicals. Fourth, for the past four decades, modern pest managers have made decisions using knowledge of population dynamics and thresholds. Fifth, and currently ongoing, public research and technology transfer is being used to fine-tune IPM programs to meet food safety and security needs for a growing world population. Here we provide an historical perspective on the evolution of research and its applications in stored-product entomology to identify cost-effective research priorities for the future.

EARLY TECHNOLOGY AND TRANSITIONS TO THE PRESENT

Stored products include all postharvest agricultural products that do not require refrigeration and can be stored for several months under proper conditions. Ancient literature and archaeological evidence indicate some of the first technologies for protecting harvested grains from insects included hermetic sealing to lower O_2 and increase CO_2; sieving or floatation to remove infested kernels; burning of badly infested grain; burning sulfur as a fumigant; adding chalk dust, ashes, and charcoal as desiccants; adding olive oil; and using toxic botanicals (106). By the Bronze Age (circa 3,200–600 BCE), large-scale storage and movement of commodities was evident, and potential losses due to insects were more likely.

Storage Structures

Many types of storage have been used throughout history (**Figure 1**). The first agricultural communities may have been in semiarid river valleys where crops were irrigated and the dry climate reduced insect problems (114). As storage of cereals spread to cooler and wetter regions in Europe, grain drying became necessary. Pit storage, the most ancient method, is still used in the Middle East and Africa, but not in the Americas. Pits that are wide at the bottom and narrow at the top are lined with straw, which is more hydroscopic than grain and keeps the soil moisture away from the grain.

Families and small villages have stored small quantities of grain in baskets or mud jars (**Figure 1*a***) and larger quantities in granaries built of thatch, mud bricks, or other locally available materials. Some early elevators were made of wood, and the first grain elevator was built in Buffalo, New York, in 1842. These elevators received grain at ground level and moved it upward in buckets spaced along a vertical conveyer belt and then horizontally for distribution and gravity loading into grain bins. Other innovations for grain storage, handling, and marketing developed in North America were also eventually adopted in Europe and other industrialized countries (**Figure 1*c–e***). However, covered outdoor bag stacks (**Figure 1*b***) or bag storage in enclosed warehouses are still used in several countries.

Botanicals

Plant products such as powders or extracted oils from leaves, roots, flowers, fruits, or seeds have been traditionally used for pest control (83). Fatty acids, phenols, alkaloids, and terpenes are the

Figure 1

Various storage systems. (*a*) Mud jar referred to as a *gota* and used by African smallholders; (*b*) outdoor bag stacks; (*c*) steel bins with aeration and fumigant recirculation; (*d*) concrete elevator in a small midwestern US town; (*e*) large concrete elevator system with processing and shipping; and (*f*) hermetic small-bag storage, the Purdue Improved Crop Storage system. Images courtesy of (*a*) Tesfaye Tadesse, Kansas State University, (*b*) George Opit, Oklahoma State University, (*c*,*d*) Edmond Bonjour, Oklahoma State University, (*e*) US Department of Agriculture/Agricultural Research Service, Keith Weller, and (*f*) Tom Campbell, Purdue University.

most common active ingredients. Plant products can be contact or fumigant insecticides, repellents, or antifeedants, or they can act by reducing reproduction. Of existing plant products, two are commercially available and used for stored-product protection (55). Pyrethrum from chrysanthemums has been produced commercially for more than 150 years. Small-scale producers in India have cultivated neem, *Azadirachtha indica* A. Juss., for relatively small markets, but commercial development has expanded in recent years in response to market demands.

ASH AS NATURAL INSECTICIDE

Cowpeas are traditionally mixed with ash, stored in a mud granary or a clay jar, compressed by tapping down, and may then be covered with a final top layer of ash (149). A minimum of three parts ash to four parts cowpeas has been used to prevent population growth of *Callosobruchus maculatus* (F.), and a 3-cm layer of ash on top of stored seeds prevents infestation by adults. Ash does not affect seed germination or the taste of cowpeas if it is rinsed off prior to consumption. Ash may function as a physical barrier, but it may also desiccate *C. maculatus* eggs and adults or clog adult spiracles and tracheae, thus causing suffocation.

Desiccant Dusts

Though generally nontoxic, siliceous dusts can absorb the lipid coating from insect cuticles, which results in mortality due to desiccation. Some of the earliest research on insecticidal dusts was done in Germany (151). Prior to the 1950s, clay dusts, sand, or silica gels were used more extensively than diatomaceous earth (81). Ash is another traditional method used in northern Cameroon to protect cowpeas, *Vigna unguiculata* (L.) (Walpers), against insects during storage (149) (see the sidebar titled Ash as Natural Insecticide). Korunic (81) reviewed the research on the effectiveness of diatomaceous earth on 15 species of stored-product insects and concluded that tolerance varied considerably among insect species. Species of the genus *Cryptolestes* were the most sensitive, followed by those of *Sitophilus*, *Oryzaephilus*, *Rhyzopertha*, and *Tribolium*.

Taxonomy and Diversity

A total of 1,663 insect species have been reported to infest postharvest agricultural commodities, but only a few hundred compose the most widely distributed, most economically important, and best-known pests (63). Fifteen percent of stored-product insect pests were taxonomically described prior to 1800, the majority (57%) between 1800 and 1899, and 28% more recently. However, if only the 430 most damaging species are considered, the percentages for these three time periods are 37, 51, and 12%, respectively.

Results from 26 studies found 61 insect species at grain elevators (59), 15 studies recorded 119 species at mills (89), and 12 studies found 155 species at retailers (62). The diversity of insect species apparently increased as commodities moved through marketing channels. Of the 223 insect species recorded by 53 studies, 40 were found at elevator, mill, and retail locations; 10 only at elevators; 50 only at mills; and 92 only at retailers.

Prior to written history, many stored-product insect species had nearly worldwide distributions as a result of human migration and trade (79). Archaeological evidence indicates that stored-product insects were not present in England before the Roman occupation. However, this evidence is predominantly from northwest Europe, so more fossils are needed from across the Palaearctic and North Africa. Hagstrum & Subramanyam (62, 63) discussed how *Acanthoscelides obtectus* (Say), *Caryedon serratus* (Olivier), *Cynaeus angustus* (LeConte), *Prostephanus truncatus*, *Trogoderma granarium*, and *Zabrotes subfasciatus* (Boheman) have expanded their geographic and/or host ranges throughout recorded history. *Ephestia kuehniella* Zeller was native to Southwest Asia (85) and was reported in Germany in 1877, Belgium in 1884, England in 1887, Canada in 1889, the United States in 1892, and Australia in 1893 (52, 118). Some of the most common and serious stored-product insects mentioned above, and also common storage mites, are highly adapted to habitats with human-stored foods and can be considered domesticated pests.

Loss Assessment

Parkin (107), in the first volume of the *Annual Review of Entomology*, reviewed the assessment and reduction of grain weight loss due to stored-products insects. Mostly anecdotal prior to 1970 (69), estimates now indicate losses below 5% over an average storage period (27). Recent threats to food security include the introduction during the 1980s of *P. truncatus* to Africa from Mesoamerica, adoption of high-yielding crop varieties with less insect resistance, and shortages of wood used for smoking and the construction of traditional storage structures. In most districts of Ghana, smoking had been the most commonly used method of pest control for maize stores (25).

Since 2012, rather than relying on a single average value, the African Postharvest Losses Information System (**http://www.aphlis.net**), initiated by the Joint Research Centre of the European Commission, has provided estimates of postharvest losses according to crop and country as well as particular to the climatically different provinces in Sub-Saharan Africa (69). Postharvest weight losses are useful for formulating agricultural policy, developing postharvest loss-reduction projects, and predicting food supply in developing countries. In industrial countries, economic losses due to insect contamination have become more important than weight losses. In the United States, the Food, Drug and Cosmetic Act of 1938 authorized the Food and Drug Administration to prevent interstate shipment of food containing filth or that was prepared, packed, or held under unsanitary conditions. To help support regulations, extensive research focused on identifying the species of insect cuticle fragments found in food and determining defect action levels for many commodities (90). Inspection programs began with foods eaten without further cooking such as those sold by bakeries (84). Flour mills were next. On the basis of studies of wheat and wheat flour (67) as well as corn and cornmeal (68), the Clean Grain Program was initiated. Another program to inspect local grain elevators began in 1952. Conferences on grain sanitation have also been held to help reduce insect problems.

Legal or Regulatory Control

Regulatory controls to prevent the introduction of exotic pests began well before modern pesticides were available and included education, inspection, quarantine, and eradication (1). *Cylas formicarius elegantulus* (Fabricius), *Phthorimaea operculella* (Zeller), and *T. granarium* (Everts) are regulated species in the United States and other countries. In 1919 and 1937, eradication programs for *C. formicarius elegantulus* were undertaken in the United States (102), and more recently in Japan (95). In the 1950s and 1980s, eradication of *T. granarium*, the famous khapra beetle, was undertaken in the United States (98), and more recently in Australia (40). In Africa, *Prostephanus truncatus* (Horn) is a regulated species, whose regulatory control has been described by Tyler & Hodges (146).

AGE OF CHEMICAL CONTROL

Fumigants and residual insecticides were introduced in the late-nineteenth and early-twentieth centuries. Pesticide regulation also has a long history (35). In the United States, the 1910 Federal Insecticide, Fungicide, and Rodenticide Act was enacted primarily to protect consumers from misbranding. Arthur & Rogers (9) discussed the impact of regulations on the management of stored-product insect pests. International regulations have had an important impact on international trade (32).

Fumigants

Fumigants are gaseous pesticides. These acute toxins rapidly mitigate an infestation while leaving very little to no detectable chemical residue. Carbon disulfide was first used in 1854, but it was not used to treat grain until 1879; hydrocyanic acid was first used in 1886, chloropicrin in 1907, ethylene oxide in 1927, and methyl bromide (originally as a fire extinguisher) in 1932 (9, 130). Phosphine had been used in Germany for many years before becoming the dominant fumigant worldwide. To increase the uniformity of fumigant distribution in large grain bins, recirculation or closed-loop fumigation was used in the early 1900s in Europe (94) and recently in the United States (77, 86). With the recent ban on methyl bromide as an ozone depleter and as insects have become resistant to phosphine, research has focused on sulfuryl fluoride as a replacement (101).

Spot or local fumigation of equipment between full mill fumigations were recommended in 1936 (34). Early fumigants did not penetrate accumulated food residues, so individual pieces of equipment were cleaned and sealed off prior to fumigation. However, insects from unfumigated equipment reinfested fumigated equipment. As more penetrating fumigants became available, less time was required to clean equipment prior to fumigation. Fumigating all the equipment at one time has improved the effectiveness of spot fumigation, and in some cases, spot fumigation has replaced full mill fumigation. In-transit fumigation of grain was developed to treat insect infestations discovered during loading of railcars and ships (33). The use of shipping containers had provided an additional opportunity for in-transit fumigation (56).

Residual Grain Protectants

The idea of a grain protectant involves applying a residual pesticide to the entire grain mass at the time of storage to prevent infestation while the grain is held in storage. Since 1945, lindane has been applied directly to stored grains, as a residual treatment in storage areas and as an aerosol (96). Between 1949 and 1965, lindane was mixed with grains in African countries, India, and Brazil. Lindane was applied to storage areas in England, the United States, and Canada. Synergized pyrethrum was generally used before 1959 to control insects in stored peanuts, but by 1961, it had been replaced by malathion (134). In 1958, malathion was first registered in the United States. In the early 1960s, malathion resistance in the red flour beetle, *Tribolium castaneum* (Herbst), was first recorded in Nigeria, then later in the United States, Egypt, and Australia (153). A world survey of pesticide use in 1976 added bioresmethrin, bromophos, carbaryl, chlorpyrifos methyl, DDT (dichlorodiphenyltrichloroethane), diazinon, fenitrothion, fenthion, and pirimiphos methyl to the list of chemicals used to control stored-product insects (21).

Aerosols

Aerosols are active chemical ingredients delivered via minute liquid droplets to an indoor space and thus lack the penetrating ability of fumigant gases. In 1957, dichlorvos as an aerosol was first used against exposed tobacco pests in warehouses (14). Synthetic pyrethroids and organophosphates have been used to control stored-product insects in transport vehicles. Pyrethroids alone or combined with insect-growth regulators such as methoprene, hydroprene, and pyriproxyfen were later investigated as potential aerosols.

The cost of using aerosol insecticides is less than that of fumigation with methyl bromide and sulfuryl fluoride or of heat treatment. Less sealing is required for aerosols than for fumigation. Facility shutdown for aerosol treatment is much shorter ($\leq$12 h) than that required for fumigation or heat treatments (24–34 h). Aerosols are being used more widely in food storage and food processing, perhaps in response to the ban on methyl bromide. Nevertheless, aerosols lack the penetrating ability of fumigants, and the toxic activity for many of their active ingredients is short-lived at best (8).

Insecticide Resistance

Worldwide, many stored-grain pests have evolved resistance to commonly used insecticides (21). Resistance was initially slow to develop in insects in stored products because all stores in a particular locality were rarely treated and susceptible insects from neighboring stores, farms, and markets were frequently reintroduced to the fumigated storages (108). As a result of commerce, however, resistance has spread. In Africa, *T. castaneum* has become resistant to lindane and malathion (39). In Asia, *Rhyzopertha dominica* (F.), *T. castaneum*, *Sitophilus oryzae* (L.), *Oryzaephilus surinamensis* (L.), and *Cryptolestes ferrugineus* (Stephens) are resistant to phosphine (138); *T. castaneum* is also phosphine resistant in Brazil (111). Local selection and insect dispersal have further facilitated the resistance of *O. surinamensis* and *R. dominica* in Brazil. More recently, phosphine resistance has become prevalent in North America, years after its prevalence was reported in other countries (23, 105).

T. castaneum demonstrated resistance to a juvenile hormone analogue before it was used as an insecticide (38), and *Lasioderma serricorne* infesting tobacco in the southern United States has also become resistant (13). Insects with resistance genes have been found decades after an insecticide has been discontinued (e.g., 4). Thus, pest populations have the potential to become resistant to many common insecticides, and only new chemistry can provide acceptable control in many cases.

Noteworthy cases of resistance among stored-product insects have resulted in breakthroughs in our understanding of insect genetics and physiology. The *T. castaneum* genome provided a tool for biologists to address numerous topics (144) including the genetic basis of phosphine and pyrethroid resistance (23, 127, 154). Research on the mechanism of resistance of pyralid moths to the pathogen *Bacillus thuringiensis* Berliner has been important for pest control (147).

BIORATIONAL METHODS

Biorational management of stored-product pests was reviewed by Phillips & Throne (110). Ionizing radiation is very effective against stored-product insects (141), but because of costs and consumer concerns about food irradiation, it generally has not been used commercially to disinfest stored commodities. Other key historical aspects of relevant tactics are summarized below.

Grain Aeration

By lowering grain temperatures, cooling with aeration fans can substantially delay the development of insect pests. Power ventilation was not justified to cool corn (70), but Kline & Converse (80) found that aeration was cost effective for wheat. According to 22 extension bulletins published between 1964 and 1998, aeration is used to avoid moisture migration, whereas pesticides are used to control insects (115). More recently, however, aeration has also been used to control insects. In simulation (47) and field (117) studies, automatic controllers, which turn on fans only when the outside temperature is sufficiently low to cool grain, improve the effectiveness of aeration in managing insect pests. Grain chilling with refrigerated air was first tried in the United States in the late 1950s, and there are seven major worldwide manufacturers of grain chillers (91). However, the high costs of grain refrigeration limit its application to special situations.

Extreme Temperature Treatments

Insects do not markedly regulate their body temperature. Thus, extreme temperatures reduce their survival (44). Cold kills insects more slowly than does heat, and temperatures between −1 and 3°C cause death in hours or days (44). Effective heat treatments require temperatures between 43 and 46°C throughout a commodity or facility (62), though commodities and heat-sensitive equipment may need to be removed from a facility to avoid being heat damaged.

Overall, the use of heat treatments for stored-product pest control has had a circular history (66, 137). Once replaced by methyl bromide fumigation, heat treatments are now replacing methyl bromide, which is being banned as an ozone depleter. Heat treatments were investigated by Monceau in 1762 when Angoumois grain moth first became a problem in France and by Webster in 1883 when the same species was a problem in the United States. In 1931, Grossman used heat in corn bins in Florida. In the 1900s, heat treatments were used in flour mills in Kansas, Montana, and Ohio.

In India, brick ovens as well as smoke generation were recommended to disinfest an empty warehouse used for bag storage (113). Heat can also be used to disinfest metal (140) and concrete (104) grain bins (**Figure 1*c,d***). Fluidized beds, which suspend grain in hot air, have been used to heat moving grain (43), and the use of high-frequency microwaves to heat grain has been investigated (65). Grain must be adequately cooled before long-term storage because high temperatures can damage grain. Hansen (66) reviewed the use of solar heating in excess of 50°C to disinfest stored commodities.

Sanitation, Impact, and Exclusion

The cleanup of spilled product that can harbor insects and the exclusion of insects from food and storage or processing facilities are the primary preventive methods of stored-product IPM. Building design is important for effective sanitation and exclusion (71). The use of vacuum cleaners has been promoted in both grain storage (72) and food processing (6). Cost-benefit analysis has been reported for sanitation programs on farms (3) and in flour mills (24). Quantitative research on the effectiveness of sanitation for stored grain (73, 99, 116), food processors (148), and retail stores (119) indicates that sanitation does not eliminate insects but it does make other methods such as pesticides (7) or heat treatments (17) more effective because it eliminates some insect refuges.

Impact machines to kill insects in fast-moving grain and grain products in mills are 98–100% effective against *S. oryzae*, *T. castaneum*, and *R. dominica* (30). Impact machines are used on dry wheat to release insects from kernels before a scourer aspirator is used to remove the insects (5). Insect mortality depends on rotor speed and the throughput of commodity (112). Impact machines were used by 95% of 66 companies in 19 countries, prior to storage (43%), shipping (5%), and packaging (33%) as well as during milling (40%), and 90% of millers found them to be effective. The impact of simply moving the grain is also sufficient to kill insects (62).

As commodities are moved through marking channels, packaging should provide protection from insects and other depredations. Research on insect-resistant packaging began during the late 1920s in Germany and early 1940s in the United States. Zacher (150) investigated the influence of packaging on the likelihood of commodity infestation. Stracener (135) found that multiwall paper bags provided 80% better infestation prevention than burlap bags. Essig et al. (42), Linsley (87), and Rosoff (121) each investigated the ability of insects to penetrate various packaging materials. Insects easily penetrate paper and cellophane, but multilayer construction improves resistance (97). Polyester, developed in 1941, resists insect penetration but costs more than paper. Food packaging treated with methoprene, a food-safe insect-growth regulator, is now commercially available and has received regulatory approval in the United States, and insecticidal-controlled atmospheres can be used in small food packages that are relatively gastight.

Biological Control

The natural enemies of insects are known from most stored-product insect pests. Hagstrum & Subramanyam (63) reported 468 species of natural enemies, and research on biological control dates back more than 100 years. For example, Froggat (53) reported the ichneumonid wasp *Venturia canescens* (Gravenhorst) controlled *E. kuehniella* in a flour mill. According to a review of the literature on biocontrol in stored products, for 13 species of natural enemies attacking 19 species of stored-product pests, 163 of 212 estimates of pest mortality indicated rates between 70% and 100% and more than half were between 90% and 100% (62). Releasing *Theocolax elegans* (Westwood) in stored wheat reduced *R. dominica* by 95% (46) and the resulting insect fragments in flour milled from this wheat (45). A private company selling parasitoids within the European organic food trade, including distribution to individual consumers, has been successful (50), and several large commercial insectaries in North America have mass-reared parasitoids and predators for use in large-scale release in stored-product settings. The inoculative release of a predator against *P. truncatus* in Benin is an example of a successful large-scale use of biological control for stored grain (15).

Pheromones

In an 1898 entry to his *American Miller* column, Johnson (76) described the calling position of the *E. kuehniella* female as an abdomen protruding between wings. Norris & Richards in 1933 (103) and Dickins in 1936 (36) found that males were attracted to the pheromone emitted by calling females. Changes in the flight behavior of the male approaching a calling female pyralid moth have also been described (92). The sex pheromone of the black carpet beetle *Attagenus unicolor* was identified in 1966 (129) and was among the first insect pheromones identified and synthesized. Another pheromone common to several species of pyralid moths was next identified (16). Pheromone traps and lures for stored-product insects were commercially available by the mid-1980s (109), and at present, pheromone traps are used to detect and monitor populations of key pest species as part of routine pest control and IPM programs worldwide (20, 142). A rapidly growing application for pheromones in stored-product IPM is the use of government-approved, commercially available pheromones to control pest moth populations via mating disruption, mass trapping, and variations of attract-and-kill technologies as reviewed by Savoldelli & Trematerra (126). In the United States, mating disruption for moth control is replacing aerosols and other pesticide applications in processing and value-added product storage.

Controlled and Modified Atmospheres

The use of CO_2 to control insects in stored maize was recommended in Australia nearly 100 years ago (54; for a review of more recent work, see 100). Controlled atmospheres, in which gasses are maintained at killing concentrations, e.g., high CO_2 and/or low O_2 for short periods, are now available from commercial suppliers for use in large buildings or in well-sealed grain storages. Modified atmosphere applications exploit aerobic respiration to increase CO_2 and decrease O_2 and were used in the earliest pit storages. Recently, Purdue Improved Crop Storage bags (**Figure 1*f***) were distributed along with training to smallholder farmers throughout western Africa for hermetically storing several-hundred kilograms per bag of edible beans, cowpeas, cereal grains, or peanuts (11).

Low-Risk Chemicals

The use of residual insecticides has evolved from low-risk natural pyrethrum to synthetic and potentially dangerous neurotoxins. Today, safer juvenile hormone analogs, diatomaceous earth, and spinosyns are used. Methoprene, hydroprene, pyriproxyfen, chlorfenapyr, and diatomaceous earth are currently registered and marketed commercially, and spinosad has been formulated and registered for use on grain (8, 93). Research has been published on the efficacy of another insect growth regulator (novaluron), a newer spinosyn (spinetoram), and neonicotinoids (imidacloprid and thiamethoxam) as residual insecticides for use with stored products (82, 123). Thus, numerous effective, low-risk chemical products are available for stored-product applications, and their use could increase in the near future.

Host-Plant Resistance

Insect-resistant varieties have been investigated for almonds (133), cereal grains, and edible legumes (2, 37, 139), and potatoes (26, 120, 145) during storage, but to date, no fully recognized resistance cultivar has been bred. Host-plant resistance mechanisms include antifeedant, antioviposition, repellent or toxic chemicals (10), as well as tight-sealing husk- or shell-resistant surface texture and seed-coat hardness. Commercial crop breeding is focused on many varietal characteristics that likely do not include resistance to storage pests.

DECISION TOOLS FOR INTEGRATED PEST MANAGEMENT

Better sampling methods and insights from life histories and ecological studies can optimize the timing of IPM. Ecological studies have improved our understanding of how fumigants and insecticides work, i.e., the impact of incomplete coverage on their efficacy, how important refuges from insecticide are for insects, the role of insect repellence, the value of sublethal effects, and the influence of insect food availability and type (62). Private consultants and extension programs can be important in establishing effective IPM programs (64).

Life Histories and Population Ecology

Early works on insect life histories were descriptive (see the sidebar titled Types of Insect Reproduction). The durations of insect developmental stages, mortality, and fecundity were then determined at room temperature. Beginning in the early-twentieth century, life histories were determined at several temperatures and relative humidities, and they were eventually described using mathematical equations and computers to predict population growth (62). Like other insects, stored-product insects tend to spend a fixed percentage of their total development in each developmental stage (75), but humidity can shorten their time in the larval stage and stress can increase the number of larval instars (41). For more information about the use of models, see the sections titled Predictive Models for Optimal Timing and Expert Systems.

Population ecology is the study of insect distribution and abundance, and pests may infest commodities before or after storage. For some cereal grains and edible legumes whose seeds may

TYPES OF INSECT REPRODUCTION

For stored-product moths and some of the short-lived stored-product beetles (anobiids, bruchids, and dermestids), larvae accumulate food reserves for adult reproduction (62). These species generally lay 100–400 eggs over a three- to four-day period soon after eclosion, and adults live for only a few days after reproducing. For long-lived stored-product beetles, adults feed and accumulate food reserves for egg production. An adult may live for 6 months to 1 year or more, laying 1–20 eggs each day and 100–500 eggs over its lifetime.

SPATIAL VARIATION OF INSECT DENSITY

The relationship between variance and mean insect density is widely used to calculate the number of samples needed to estimate the mean with a given accuracy and to develop sequential sampling plans (62). Analyses of commodity samples and trap catch data for stored-product insects indicate this relationship is curvilinear and consistent between insect species and commodities. A linear approximation of the curve can be used when data are collected over insect densities ranging over five orders of magnitude (0.1 to 1,000). Otherwise, the slope of the line depends on the range of insect densities considered.

be infested prior to harvest, variables such as varietal resistance, modified planting or harvest time, intercropping, application of insecticides in the field, and combinations thereof should be considered because infestation moves with a crop when put into storage (62, 63). Many insect species may live in food residues in equipment and facilities and then infest newly stored or processed commodities. Residual populations are difficult to manage because stored-product insects utilize a broad range of foods and many species diapause. Following dispersal by flight or other transport, their mobility also allows stored-product insects to locate food, mates, and oviposition sites, even when these are scarce. Forty species of pyralids, dermestids, ptinids, and bruchids diapause, making them even more tolerant to adverse environments and toxic chemicals (12). The introduction of shipping containers reduced insect cross infestation of commodities during transport (51).

Sampling

In Canada during World War II when grain could not be shipped, Smallman (132) developed a scouting program for grain in long-term storage. Raney (131) developed a similar scouting program for farmers in Kentucky, and Reed (48) implemented a scouting program for elevators in Kansas. During the chemical age and even today, pest management may often follow a calendar schedule, but as IPM evolves, it is clear that regular sampling is needed to optimize the timing of pest mitigation (see the sidebar titled Spatial Variation of Insect Density).

Hagstrum & Subramanyam (62) reviewed sampling plans developed between 1985 and 2004 for bulk storage, processing, transportation, and marketing facilities. Commodity samples provide absolute insect density estimates per quantity of commodity sampled, but traps provide relative estimates of insect density based on number trapped per day. Several studies convert relative to absolute density (49, 125). Rigorous procedures have been developed for visual inspection. Several studies have used release-recapture methods to make absolute density estimates using traps. A self-marking method has been used to study the dispersal behavior of insects in food-processing facilities (18, 19, 128).

Economic Thresholds

Accurate estimation of insect density often requires more sampling than is practically feasible. However, determining whether a pest population is near the density at which economic losses occur may overcome this obstacle (62). Economic thresholds have been determined for eight insect species that infest raw commodity storages, processing plants, or retail businesses (22, 58, 88, 122, 124, 152). The thresholds for traps were higher than were those for commodity samples and lower for processed commodities than for raw commodities. Thresholds were also lower for high-value commodities and for insect species causing the most damage to commodities.

Predictive Models for Optimal Timing

Simulation models that predict population growth, age structure, and spatial distribution are powerful tools for developing the best programs for managing insect pests. Computer simulation models can predict the population growth of 14 species of stored-product insect pests and 4 species of natural enemies (62). These models have also been used to predict the effects of harvest date, aeration, fumigation, natural enemies, insecticide resistance, and other variables on insect populations. These predictive models are used in expert systems to make optimal IPM recommendations.

Expert Systems

Expert system computer programs are learning or planning aids. Containing the knowledge of many experts, these systems help users diagnose pest problems and recommend solutions. Expert systems for stored-product IPM were developed for seven countries between 1991 and 2007 (62, 143). Compton et al. (28) and Jones et al. (78) developed another expert system for pest control in bagged grain storage (**Figure 1*b***) in the tropics. Current expert systems will be useful in the short-term, but they will need to be updated and adapted across geographies and commodities to be useful to the grain and food industries. This need is especially critical, as many scientists who developed and validated these expert systems have retired or moved on to other projects.

TRENDS IN SOURCES OF RESEARCH AND ITS DISSEMINATION

Publication of research on stored-product insects by 934 authors over the past 100 years reveals that research has become geographically dispersed, with 14 countries contributing from 1911 to 1945, 33 countries from 1946 to 1980, and 65 countries from 1981 to 2015 (**http://storedproductinsects.com/history/directory-of-stored-product-insect-paper-authors-past-and-present/**). Concurrently, contributions by authors from the 10 pioneering nations decreased: 95%, 83%, and 58%, respectively. The distribution of authors among these countries was as follows: From Australia, there were 38 authors; Canada, 49; Egypt, 33; England, 92; Germany, 41; India, 79; Italy, 22; Japan, 45; Nigeria, 37; and the United States, 252.

Local conferences on stored-product entomology were held in Germany between 1925 and 1935 and in Italy from 1972 to the present (**http://storedproductinsects.com/columns/italian-pest-management-symposium-1972-2012/**). Conferences now have global coverage. The Entomological Society of America has had a symposium or informal conference on stored-product entomology at its annual meeting since 1975. The International Conference of Entomology regularly has a symposium on stored-product entomology. The International Working Conference on Stored Product Protection first convened in 1974 and meets every four years, alternating its conference every two years with the International Conference for Controlled Atmosphere and Fumigation of Stored Products, which began in 1979 and also occurs every four years. Finally, the Integrated Protection of Stored Products Conference in Europe has met every other year since 1997.

Outreach via magazine columns has a long history, such as in *American Miller* by Willis Grant Johnson from 1895 to 1907 (e.g., 76), *Northwestern Miller* by Richard Thomas Cotton from 1960 to 1965 (e.g., 29), and more recently in *Grain Journal* by Linda Mason from 1993 to 2009 and *Milling Journal* by Bhadriraju Subramanyam from 2002 to the present. For a list of these magazine columns see **https://storedproductinsects.com/columns/other-trade-journal-articles/**.

A VISION FOR STORED-PRODUCT INSECT PEST MANAGEMENT

Although more expensive, more than one IPM method may be combined when doing so is more effective than using either method alone (see table 1 in Reference 60). Research has focused on the synergism possible with such combinations. However, when one method does not provide long-term protection, another may be needed to prevent resurgence. Combinations also may be used when particular methods are most effective at different times, at different insect densities, for different insect species, or to slow the development of resistance. More research is needed on how different methods can be used sequentially in an IPM program.

The UN Food and Agriculture Organization estimates that the global human population will reach 9.8 billion in the year 2050, up 70% from an estimate of 5.6 billion in 1995. Estimates for food production needed to support that future population vary by region: Current levels will be needed for industrialized countries, whereas production will have to increase from two- to fivefold among developing countries (**http://www.fao.org/docrep/x0262e/x0262e23.htm**).

Increased crop production must include continued and effective postharvest security. Future investments of public resources to fund research on IPM for stored products will be essential to protect the world's food supply. Although much research has been done on the components of IPM programs, more research is needed on how these components can be combined, streamlined, and economized. The optimal timing of IPM actions needs to be determined. As with all agriculture, IPM decisions within stored-product systems will be put into practice when they are cost-effective, so more research on the economics of pest management is needed.

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