Insect-Fungus Associations Influencing Seed Deterioration

J. T. Mills

Research scientist, Agriculture Canada Research Station, 195 Dafoe Road, Winnipeg, Manitoba, Canada R3T 2M9.

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Interactions between insects and fungi have traditionally been studied from the perspective of the disciplines of entomology, mycology, and plant pathology with most emphasis on insect transmission of plant pathogens and the biotic components in stored grain. Entomological, mycological, and plant pathological aspects of insect-fungus interactions that have been reviewed include insects and seed production (8), disease transmission by insects (3,11), microflora of stored grain (12), and insects in stored grain (9,14,24). Some attempts have been made to study interactions in stored grain using a holistic approach, taking into account the many factors influencing the major biotic components in relation to the environment (37). As yet there are no similar studies of insect-fungus interrelationships on seeds in growing crops, although studies on the ecology of plant diseases are well known (49). No overall account of insect-fungus interactions in relation to all types of seed deterioration has been published. The objective of this contribution is to provide an overview of what is known about the influence of insect-fungus associations on seed deterioration from an ecological viewpoint.

In this review, the term *insect* includes true insects and mites, and the term *fungus* is used for the filamentous molds and yeasts. The terms *association* and *interaction* are frequently confused; *association* is used when populations of insects and fungi occur together without affecting each other, whereas *interaction* is used when one or both of the two populations has a definite influence on the other. The term *seed deterioration* includes disrupted kernel development, physical damage caused by insects, quality changes in storage, loss in germination, and loss of unemerged seedlings. The terms *community* and *ecosystem* describe levels of ecological organization. A *community* is a group of populations living in a habitat. Each population plays a role in the flow of energy and materials through an ecosystem. An *ecosystem* is formed by several communities in a contiguous area and includes living organisms and nonliving substances interacting with an exchange of materials between living and nonliving parts (35). For convenience the term *plant-soil ecosystem* is used for describing interactions between insects and fungi on aerial or subterranean parts of plants, on the soil surface, or in the soil. The terms *producer, primary* and *secondary consumer*, and *decomposer* are used to describe the different kinds of trophic levels within an ecosystem. *Producers* (eg, green plants) bring new energy into the ecosystem from the sun via photosynthesis. Seeds may be regarded as a form of dormant producer. *Primary consumers* derive their nutrients directly from producers (eg, seeds), whereas *secondary consumers* obtain nutrients from primary consumers. *Decomposers* live on dead bodies of organisms. The roles of microfloral decomposers and consumers are often confused. *Aspergillus* species colonizing dormant seeds are frequently regarded as decomposers. In reality some *Aspergillus* species are decomposers of dead seeds; others are primary consumers living on dormant viable seeds, sometimes killing the embryos. Examples of ecosystem energy flows and trophic levels are given by Sinha (37) and Zadoks and Schein (49).

To permit classification of diverse insect-fungus interactions influencing seed deterioration (Table 1), a schema (Table 2) was devised based on stage of crop development. The main stages of crop development are preharvest, harvest, postharvest, and postplanting with preharvest subdivided into anthesis and seed-enlargement phases. The interactions are further classified into several categories based on type of insect involvement, ie, whether the insect transports the fungal pathogen to the host, damages the host by feeding with mandibulate or sucking mouth parts, or participates in a symbiotic relationship. Selected examples from each category will be outlined together with the respective roles of insect and fungus and their ecological relationships.

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Preharvest Anthesis

Interactions with contaminated field insects.—Example: *Claviceps purpurea* on rye (Fig. 1B). The insects feed on moist sticky masses of honeydew produced by the fungus on the surface of the ovary (45) and carry conidia present in the honeydew to uninoculated flowers. Mercier (33) showed that conidia are present on the body surface of the fly *Sciara thomae* L. and, when ingested, pass through the gut without losing viability. Regurgitation of gut contents by flies during feeding makes them effective vectors. Insect transmission is important primarily for secondary infections and long distance transport of spores. However, the beetle *Acylomus* sp. feeds on sclerotia and may carry spores on its body to rye inflorescences where the spores can initiate primary infections (29).

The fungus produces honeydew that attracts insects, propagates itself by forming conidia, and permeates and obtains nutrients from the ovary, later replacing it with sclerotial tissue.

The ecological relationships between *Sciara thomae, Acylomus* sp., *Claviceps purpurea* (Fr.) Tul., and rye seed are depicted in Fig. 1B. The flow of energy and nutrients is from the seed (producer) to the fungus (primary consumer) to the insects (secondary consumers) as the vectors receive food benefit from the fungus, not the host.

Preharvest Seed Enlargement

Interactions with mandibulate insects.—Example: *Phytophthora palmivora* causing black pod disease of cacao (Fig. 1F). Several types of insects, each with distinct roles, are involved. Ant species, particularly *Crematogaster striatula* Emery, spread the pathogen in soil particles vertically in the trees during tent-building activities in the wet season. A nitidulid beetle *Brachypeplus pilosellus* Murr. and a fly *Chaetonerius latifemur* End. are mainly responsible for local and long-distance horizontal spread of the pathogen. These species visit black pods, transport inoculum externally on their bodies and mouthparts or internally in their feces, and colonize lesions produced by other insects. The beetle feeds directly on rotting pod tissues and the fly feeds on sugars present on black pods and pods damaged by bugs of the family Miridae. The fly is strongly attracted by sugars present on the mirid-damaged pods. Pod-wounding mirids and pod borers penetrate intact pods and permit entry of the pathogen (2,17).

The fungus invades damaged cacao pods after transportation to the site by insects and, once established, rapidly obtains nutrients from inner layers of pod husk, placenta, and seeds (4), and propagates itself by forming spores. During this process, young whole pods are often destroyed, but older mature pods may still have salvageable beans. Dead seeds and pods will later be invaded

TABLE 1. Insect-fungus interactions influencing seed deterioration at various stages of crop development

Developmental stage and type of interaction				Type of seed deterioration	Reference
Host	Insect	Category[a]	Fungus		
Preharvest anthesis					
Gramineae	*Sciara thomae* (fungus gnat)	C	*Claviceps purpurea*	Nondevelopment, shrivelling, replacement by sclerotia, degrading	(23)
Cotton	*Drosophila melanogaster* (nectar feeding flies)	C	*Fusarium moniliforme, Alternaria tenuis*	Disruption of ovary; rot	(7)
Preharvest seed enlargement					
Cacao	*Crematogaster striatula* (ant), *Brachypeplus pilosellus* (nitidulid beetle), and *Chaetonerius latifemur* (fly)	C	*Phytophthora palmivora*	Shrivelling, discoloration, non-germination, rot	(4)
Cotton	*Siteroptes reniformis* (mite)	Sy	*Nigrospora oryzae*	Nondevelopment	(28)
Peanut	*Sancassania* sp., and *Tyrophagus* sp. (mites)	C,M	*Aspergillus flavus*	Mycotoxins	(6)
Corn	*Glischrochilus quadrisignatus* (picnic beetle)	C,M	*Fusarium* spp.	Rot	(47)
Cotton	*Anthonomus grandis* (boll weevil), *Heliothis zea* (cotton bollworm), and *Lygus lineolaris* (tarnished plant bug)	M,O	*Fusarium moniliforme; Alternaria tenuis*	Boll rot	(3)
Cotton	*Lygus hesperus* (lygus bug), *Chlorochroa sayi* (Say stinkbug), and *Pectinophora gossypiella* (pink bollworm)	C,M,O	*Aspergillus flavus*	Boll rot	(5,42)
Cotton	*Earias insulana* (cotton bollworm), and *P. gossypiella*	M	*Rhizopus stolonifer*	Boll rot	(3)
Corn	*Heliothiis zea* (corn ear worm)	M,O	*Aspergillus flavus, A. niger*	Insect damage, mycotoxins	(18)
Corn	*Ostrinia nubilalis* (European corn borer)	M	*Aspergillus flavus, A. niger*	Insect damage, mycotoxin	(18)
Soybean	*H. zea* (corn ear worm)	M	*Diaporthe phaseolorum* var. *sojae*	Nondevelopment	(15)
Soybean	*Acrosternum hilare* (stinkbug)	Su	*Nematospora coryli*	Nondevelopment	(13)
Cotton	*Dysdercus* sp. (cotton stainer)	Su	*Nematospora gossypii*	Nondevelopment	(19)
Cotton	*Dysdercus* sp.	Su	*Glomerella cingulata*	Boll rot	(30)
Postharvest storage and handling					
Red pepper	*Tribolium castaneum* (red flour beetle), *T. confusum* (confused flour beetle), and *Sitotroga cerealella* (Angoumois grain moth)	C,M	*Aspergillus flavus,* and *A. niger*	Pod and seed rot, mycotoxins	(36)
Cereals and oilseeds	*Sitophilus granarius* (granary weevil), *Sitotroga cerealella,* and *Acarus siro* (grain mite)	C,M	*Aspergillus* spp. and *Penicillium* spp.	Germ damage, free fatty acids, increased mustiness, heating, mycotoxins	(14)
Postplanting					
Squash	*Hylemya platura* (bean seed fly)	M,O	*Pythium ultimum* and *Chaetomium globosum*	Germ and shoot damage	(22)
Alfalfa	*Bradysia* sp. (fungus gnat)	M,O	*Fusarium oxysporum* f. sp. *medicaginis*	Germ and shoot damage	(31)

[a] C = contamination of insects by molds, M = damage by mandibulate insects, O = oviposition damage or involvement, Su = sucking damage, and Sy = synergism.

by microbial decomposers.

The fungus, nitidulid beetle, fly, mirids, and pod borers are primary consumers. The fungus rapidly destroys pods and contents and does not contribute anything to its insect vectors. This is in marked contrast to ergot, also transmitted by contaminated insects, in which only a few kernels are destroyed and the insect vector benefits.

Feeding and oviposition by mandibulate insects.—Example: *Aspergillus flavus* on cotton (Fig. 1D). Insects provide transportation and entry for the fungus to seeds through oviposition and feeding wounds. The fungus is soilborne and wind disseminated, but it is also transported externally and internally by lygus and stinkbugs, which frequently visit cotton bolls (42). Entrance to the host is via the large exit tunnels made by mature larvae of the pink bollworm and possibly oviposition wounds made by other insects (5).

The fungus invades insect-damaged cotton bolls after transportation to the site by wind or other insects and obtains nutrients from the seed and propagates itself. When this occurs, the boll becomes rotted and aflatoxin is frequently produced.

Both the fungus and the pink bollworm larvae are primary consumers. The fungus does not benefit the insect vectors.

Interactions with piercing-sucking insects.—Example: *Nematospora coryli* on soybean (Fig. 1A). The insects transport the fungus, the yeast *N. coryli* (Peglion), penetrate pods, and inoculate developing seed tissues with the fungus. Several species of stinkbugs are involved, including the green stinkbug, *Acrosternum hilare* (Say), and the lygaeid bug, *Spilostethus pandurus* (Scop.). The stinkbugs frequently carry the fungus on their mouthparts after feeding on plants and on infested soybeans. The fungus develops within young soybean seeds and provides a reservoir of propagules for subsequent visits by the vectors (13). Both the fungus and the stinkbugs are primary consumers. The fungus provides no benefit to the vector, but relies entirely on it for transportation and entrance to the host.

Interactions involving symbiosis between insects and fungi.—Example: *Nigrospora oryzae* on cotton (Fig. 1C). The pyemotid mite *Siteroptes reniformis* Krantz stimulates fungal growth, probably by chemicals, transports spores in a special internal sac, and increases the efficiency of invasion of cotton bolls by the fungus. The fungus invades and obtains nourishment from the host, perpetuates the species through production of spores, and stimulates growth and reproduction of the mite (28). The fungus is a primary consumer and the mite a secondary consumer, as it derives its food from the fungus and not from the cottonseed host.

Postharvest Storage

Interactions with contaminated storage insects.—Example: *Aspergillus* spp. on wheat (Fig. 1G). Insects feed on intact or damaged seeds, transforming seed energy and nutrients to biomass, thus permitting insect multiplication and survival. Insects reduce seed germination by eating the germ, provide an entrance for postharvest fungi, and contaminate the grains with webbing, feces, or exuviae. Some insect species are attracted to and feed on seedborne fungi, and may transport spores of spoilage fungi upon and within their bodies (20). Insect metabolic activity results in increased relative humidity (RH), which promotes germination and development of postharvest fungi in the intergranular spaces. Insect metabolic activity in grain also frequently results in heated seeds of reduced germination, poor appearance, and low nutritional quality. About 50 species of true insects occasionally cause serious injury to grains in storage; each of these has its own ecological characteristics (14,24).

Mites feed on kernels, grain dust, or seedborne fungi; prey on other mites; or act as scavengers and saprobes (40). There are about 50 species of stored-product mites, but only a few feed directly on grain kernels, causing weight and germination loss (26). Many fungivorous mites transport spores of postharvest fungi upon and within their bodies. Because the presence of mites in stored grain makes it unacceptable as food, mites are an important factor in quality loss.

Postharvest fungi colonize seeds and by their metabolic activity, may increase the RH in the intergranular spaces permitting other postharvest fungi to develop (27). The fungi also provide food for insects and mites or increase the susceptibility of the seed to attack by other microbiota. Some species (eg, *Aspergillus candidus* Link) can kill germs very rapidly. Harman (21) has described the mechanisms of seed infection and pathogenesis in this symposium, so they will not be further elaborated here. Postharvest fungal metabolic activity often results in increased free fatty acids and other quality losses (12). Some postharvest fungi are decomposers, releasing essential nutrients bound in the protoplasm of dried seeds.

In the simplified food web for stored grain (Fig. 1G) insects (eg, the red flour beetle *Tribolium castaneum* (Herbst)), mites (eg, *Acarus siro*), and fungi (eg, *Aspergillus amstelodami* (Mang.) Thom & Church) are primary consumers. Predatory mites (eg, *Cheyletus* sp.) feeding on acarid mites are secondary consumers, as are parasitic wasps (eg, *Bracon* sp. and *Cephalonomia* sp.) feeding on larvae of stored-grain beetles and moths. Psocids and tarsonemid mites feed on fungi and are also secondary consumers. However, acarid mites can feed on fungi as well as seeds, so are both primary and secondary consumers. Not shown in Fig. 1G are tertiary consumers that include pseudoscorpions and mesostigmatid mites parasitic on rodents and birds. Excrement from the primary consumers, which are sites for luxuriant microbial growth, are also eaten by certain secondary and tertiary consumers (scavengers) (37).

Studies of interactions. Laboratory studies have included the feeding preferences of stored-grain insects and mites for particular fungi (43,48). Some fungi serve as a favorable food source for insects whereas others reduce insect growth, reproductive rates, or survival (1,16). Energy budget studies have been carried out on

TABLE 2. Classification of interactions in ecosystems as related to crop and seed development

	Stage of crop development						
	Preharvest			Harvest	Postharvest	Postplanting	
	Anthesis	Seed enlargement	Ripening	Cutting, weathering, threshing, handling	Storage and handling	Sowing	Seedling growth
Stage of seed development:	Anthesis →	Seed enlargement →	Maturation →		Aging →	Germination →	Emergence →
Ecosystem type:	← Plant-soil →				← Storage →	← Plant-soil →	
Interaction examples:	Rye Fungus gnat *Claviceps*	Soybean Stinkbug *Nematospora*			Wheat Red flour beetle *Aspergillus*	Squash Bean seed fly *Chaetomium*	

some insects including the granary weevil (10). Energy budget studies have not yet been made on postharvest fungi but attempts have been made to summarize energy flow (39).

Some studies have emphasized a deductive approach using the same samples for simultaneous measurement of many variables. The data obtained are summarized and hypotheses generated using principal component analysis (PCA) (38). The PCA screens the data to determine the main constituents, the underlying structure (if any), and order in the system. Through this analysis one can examine objectively whether most of the information contained in several subjectively chosen variables can be expressed by a few variables called principal components. PCA was used to compare criteria used by commercial grain handlers and scientists to assess rapeseed quality and to identify patterns of relationship among 28 variables measured for 177 seed samples. The samples were obtained from primary elevators across western Canada and assessed as sound, spoiled, or heated (34). The first principal component revealed a relationship among *Aspergillus* spp. and free fatty acid levels and other seed quality variables. The second component primarily represented the mite fauna and their niche requirements. PCA was also used by White and Sinha (46) to detect and follow patterns of relationship and interactions in wheat ecosystems. Wheat was stored in drums and infected with various combinations of insects. Samples were removed and PCA carried out on the data at intervals. The main finding in the lesser grain borer-rice weevil-red flour beetle-infested system was that invasion

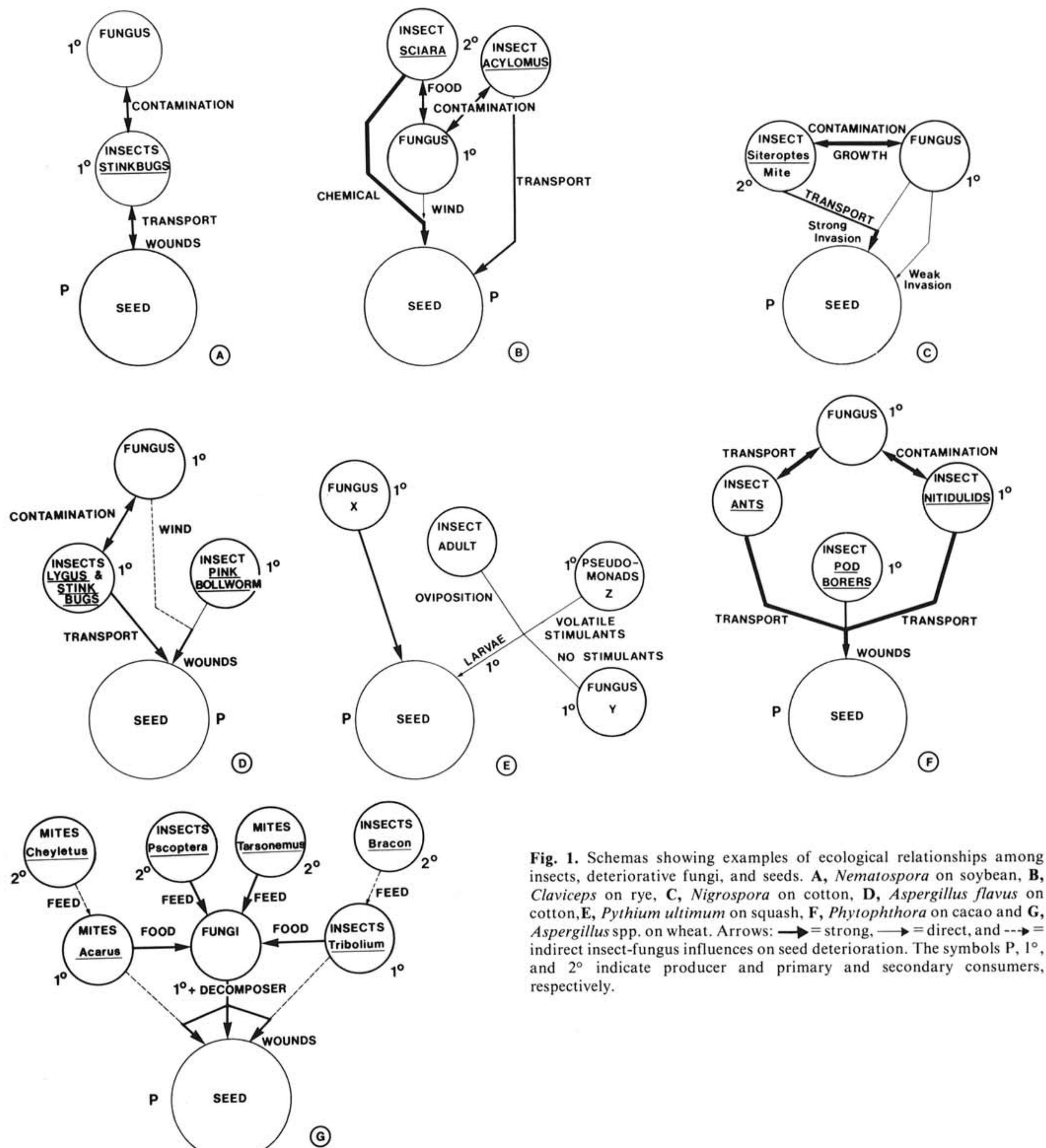

Fig. 1. Schemas showing examples of ecological relationships among insects, deteriorative fungi, and seeds. **A,** *Nematospora* on soybean, **B,** *Claviceps* on rye, **C,** *Nigrospora* on cotton, **D,** *Aspergillus flavus* on cotton, **E,** *Pythium ultimum* on squash, **F,** *Phytophthora* on cacao and **G,** *Aspergillus* spp. on wheat. Arrows: ➞ = strong, → = direct, and ---> = indirect insect-fungus influences on seed deterioration. The symbols P, 1°, and 2° indicate producer and primary and secondary consumers, respectively.

by *Aspergillus* between 18–24 wk coincided with endosperm and germ damage of seeds by insects and increased seed moisture.

Detailed studies of seed deterioration in granaries usually require the monitoring of abiotic and biotic changes occurring within a particular granary with time. Sinha et al (41) studied the interrelations among temperature, moisture, and viability of grain, and mites, insects, and fungi from 8,000 samples collected from wheat bulks every month for 8 yr. Thirty-two variables were measured for each sample and the results subjected to PCA. The first principal component was a measure of general aging of the grain and fungal succession. The second and third components were measures of the major arthropod populations interacting with factors in the physical environment.

Postplanting

Interactions with mandibulate soil insects.—Example: *Pythium ultimum* on squash (Fig. 1E). The adult bean seed fly, *Hylemya platura* (Meigen), oviposits eggs near germinating seeds that serve as food for the developing larvae. The larvae damage the young developing shoot and seed. *Pythium ultimum* Trow. and other *Pythium* spp. already present in the soil cause seed rots and damping off (22).

Pythium (Fig. 1E, X) invades and obtains nutrients from the host and propagates itself by asexual or sexual spores. *Pseudomonas* (25) (Fig. 1E, Z) on the seed produces substances that stimulate oviposition of the bean seed fly. *Chaetomium globosum* Kunze ex Fr. (Fig. 1E, Y) does not produce such substances, and thus its development on seeds prevents attacks on the host by the bean seed fly.

The fungi, *Pythium* and *Chaetomium*, and the larva of the fly are all primary consumers as they obtain nutrients directly or indirectly, in the form of exudates, from the host. The larvae feed directly on the growing seedling, and probably use the pseudomonad-modified exudates only to find the host seedling.

Environmental Effects

Moisture, temperature, food, and habitat protection are the four basic requirements needed for associations to flourish. If these requirements are examined in relation to stages of crop development, food might be limited during anthesis, whereas during seed enlargement moisture, temperature, food, and habitat protection are optimal. Between crop ripening and storage, moisture is declining and sometimes limiting. During storage there is ample food and adequate protection, but generally low or variable moisture depending on temperature fluctuations in the bin. After sowing, food, habitat protection, and moisture and temperature are generally optimal.

Most of the interactions in Table 1 occur during the stage of seed enlargement when young seeds form ideal substrates for insect and fungal development. The seeds have a higher moisture content and increasing nutrient content, are easily located in monocultural cropping systems, and field temperatures are ideal for microbiotic development.

Associations occurring during storage are possible at limiting moistures because some of the fungi can develop at low RH and many of the insects (eg, the hypopus stage of mites) are specially adapted to survive dry conditions. Further, some insects (eg, the maize weevil) are adapted to lay their eggs in ripening, but still moist, crops in the field and the larvae develop during storage (24).

Few insect-fungus associations involved with deterioration of seeds after sowing are documented. This is surprising because moisture, food, and habitat protection are optimal and conditions appear ideal. Possibly soil antagonisms, competition from other fauna and flora, lysis, difficulty for the insect to find the subterranean host, and difficulty in discovering such associations might be reasons for the low incidence reported. The sensitivity of insects to host attractants appears to be of prime importance in this type of association.

Importance of the Soil

The soil provides a central link between seed-deteriorating organisms and the aerial and subterranean plant parts and with grain in storage. Many of the organisms involved with deterioration interactions originally occurred in or near the soil (eg, postharvest fungi on decaying vegetation and stored-product insects on decaying wood and bird nests) (32). The soil provides a reservoir of fungal propagules (eg, sclerotia of ergot and *Phytophthora palmivora*) and of insects as eggs, larvae, or pupae. In addition, many insects live on alternate hosts growing in soil; for example, stinkbugs live on cruciferous and other hosts before invading soybeans later in the season (44).

Concluding Remarks

The roles of insects and fungi in seed deterioration have been described from an ecological viewpoint by presenting increasingly complex examples. More information is needed on the interactions between biotic components in agro-ecosystems, particularly within soil. Such information could lend to better seed management through improved predictive ability and control measures for seed deteriorating organisms.

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