Chapter 4

BIOLOGICAL AND BIOTECHNICAL ADVANCES FOR INSECT MANAGEMENT IN PEANUT

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BIOLOGICAL CONTROL AND BIOTECHNOLOGY IN ENTOMOLOGY

Biological Control in Peanut Entomology

Insect pests have evolved and adapted with crops since mankind first harvested seed from a wild plant species to cultivate it for his personal use. Crops were initially planted in small areas and were often intermingled with other crops or weeds. As agriculture evolved through the centuries, farmers planted larger and larger hectarages of individual crops in monocultures. Today, many agricultural crops, including peanut, are monocropped and are treated with herbicides which further reduce plant species diversity.

The wild ancestors of most agricultural crops are little damaged by pest insects (Painter, 1951). Three important reasons for the 'apparent immunity' in feral plant populations such as *Arachis* spp. are: (a) the evolution of chemicals and/or morphological characters in wild plants that decrease their suitability to insect pests (Price, 1984), (b) the coevolution of natural enemies with pests that prevents pest populations from reaching outbreak levels in diverse ecosystems (Huffaker *et al.*, 1974; Risch, 1987; Horn, 1988), and/or (c) alterations in a herbivore's host-finding behavior in more diverse ecosystems (Risch, 1983).

Modern agriculture is characterized by monoculture on large contiguous areas of land. Such systems provide an almost unlimited supply of food for pest insects, thus voiding the limiting factor(s)—i.e., the resource in shortest supply—found in more diversified habitats. Furthermore, most management inputs in modern agriculture do not consider their impact on insect pests, but are primarily concerned with providing a favorable environment for growth and production of the monocrop. Insects in a pest population respond directly to these inputs, both behaviorally and physiologically, and the result is often an increase in pest density (Rabb *et al.*, 1984). Nevertheless, natural enemies of insect pests are the first line of defense against plant injury in today's large, monocropped fields. Pest populations are usually maintained below an economic level by their endemic natural enemies, as exemplified by Sears and Smith (1975) in their study of the corn earworm, *Helicoverpa* (=*Heliothis*) *zea* (Boddie), on peanut in Texas.

Host plant resistance is also a 'biological' means of reducing pest density. Plants with resistance to major insect pests are an important component of

many agricultural systems and will become even more important in the future with society's concern for agricultural pollution and environmental quality. Insect-resistant crops may be the primary tactic in a pest management system, or may be used in conjunction with other management practices, e.g. the use of reduced rates of pesticides in concert with plant resistance (Campbell and Wynne, 1985). The use of insect-resistant plants is especially important for crops grown in developing nations where literacy and economics limit the implementation of other more costly or technologically advanced management tactics.

Biotechnology in Peanut Entomology

Biotechnology in agriculture is the use of technologies based on living systems to enhance crop production or assist in the management of crop pests such as weeds, pathogens, or insects. Biotechnological advances in entomology have occurred rapidly in the last decade. However, their application to peanut entomology has lagged behind that of other crops, such as cotton (*Gossypium hirsutum* L.), soybean [*Glycine max* (L.) Merrill], and corn (*Zea mays* L.) that are grown on much greater hectarages. For example, considerable research has been conducted on mass rearing and release, importation, and manipulation of natural enemies of *Helicoverpa* on cotton (Anonymous, 1986). Likewise, synthetic pheromones, which are chemicals that duplicate the sex attractants produced by insects, have been studied extensively for mating inhibition or for predicting potential infestations in cotton (Latheef *et al.*, 1991).

Similarly, new biotechnologies such as recombinant DNA, gene transfer, embryo manipulation and transfer, plant regeneration, tissue culture, and somatic variation are also receiving much greater attention on insects associated with major agricultural crops, rather than on peanut. Several of the technologies such as transfer of the gene for Bt-toxin (the δ-endotoxin of *Bacillus thuringiensis* Berliner), proteinase-inhibitor genes, and modification of insect baculoviruses have direct application for improving integrated pest management (IPM) systems for insect pests of peanut, and will be discussed later.

CHANGES IN INSECT MANAGEMENT

Evolution of Integrated Pest Management (IPM)

IPM has been used to manage pests in peanut since the early 1960s. This approach uses all available techniques to manage pests below an economic injury level and has succeeded in improving the yield of peanut while reducing the number of applications of insecticides (Rajotte *et al.*, 1987). The philosophy and application of IPM both in the U.S. and internationally have been reviewed (Sterling, 1984; Kiss and Meerman, 1991). Pesticides have been the primary management tactic for peanut pests. IPM in peanut has primarily emphasized treatment of pests after the problems occur, although there are alternatives to this approach.

In the U.S., insect control for row crops was described by Doutt and Smith

(1974) as a sequence of phases. The history of cotton production in the U.S. is an excellent example of these phases and serves as a warning as to what must be avoided in the development of pest management schemes for peanut. The first phase of cotton production in the U.S. was the "Subsistence Phase" in which cotton was grown under nonirrigated conditions in subsistence agriculture in the 1880s. Phase two, termed the "Exploitative Phase", involved the use of irrigation and the introduction of crop protection measures to safeguard the crop in the 1940s and 1950s. Unfortunately, this phase relied heavily on the repeated application of toxic insecticides to control pest insects with little regard for long-term changes in soil productivity or environmental quality. Next, the "Crisis Phase" usually occurred after a number of years in the exploitative phase. An example of this is U.S. cotton in the 1960s and 1970s. The heavy and repeated use of pesticides eventually permitted insect pest populations to become resistant to the insecticides, so that a cycle was created where increasingly higher application rates and more applications of insecticides were needed to control pests. Secondary pests, which are insects that are not economically important until beneficial arthropods are destroyed, were unleashed and became major pests. This combination of insecticide resistance in pest insects, pest resurgence, and secondary pest outbreaks results in greatly increased production costs because of the increased applications of insecticide.

The inevitable outcome of the crisis phase in cotton was the "Disaster Phase", characterized by an increase in production costs and decline in yield to the point where some farmers could not profitably produce a crop. The disaster phase usually affects farmers using marginal land and production practices first, but it may eventually make the crop unprofitable for even the best farmers.

The final phase of crop protection is characterized by the "Integrated Control Phase" where insecticides are used only when economically justified and all available techniques are used to manage insect pest populations below an economic threshold. Attempts are made to modify environmental factors that permit insects to achieve pest status and to use management practices that have a minimal deleterious impact on beneficial insects, insect pathogens, and the environment.

The use of pesticides has been the primary control tactic for management of pests in most row crops, a tactic that may not be ecologically sound. A different approach for managing pest populations is, therefore, needed because of increasing concerns over environmental pollution, such as pesticide contamination of aquifers under sandy soils in many peanut fields. Farmers must reduce their dependency on pesticides if they are to meet the public mandate for reduced contamination of the environment. Effective IPM systems must evolve that incorporate tactics that provide safe, environmentally compatible, and effective management of pests with a reasonable profit margin and they must be sustainable. Pedigo and Higley (1992) listed four goals for IPM: (a) reducing pest status, (b) ensuring producer profitability, (c) attaining environmental compatibility, and (d) producing sustainable

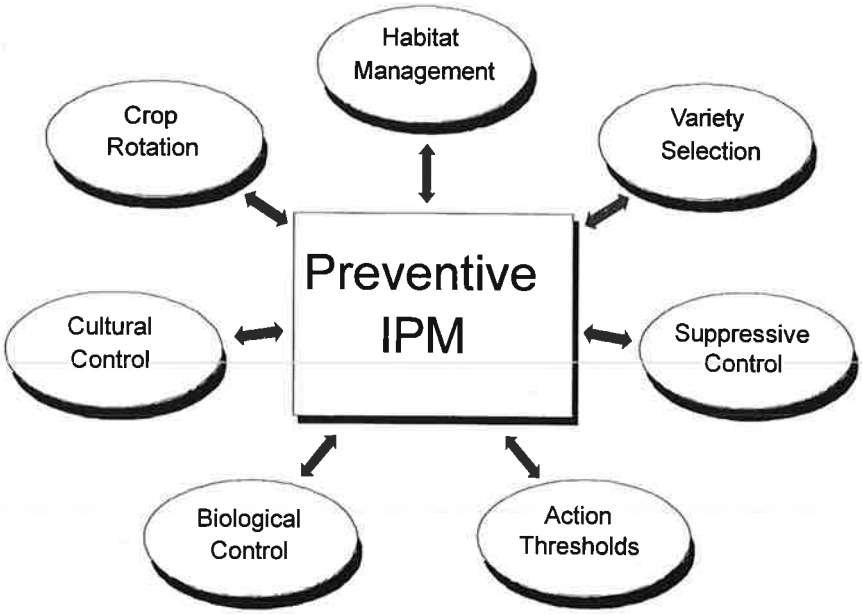

Fig. 1. Conceptual diagram of preventive pest management showing components contributing to its development (after All, 1989).

solutions to pest problems.

Preventive pest management seeks to prevent outbreaks by altering the agroecosystem before pest invasion (Fig. 1). Pedigo (1992; p. 11) stated:

> Ecologically, preventive tactics aim to prohibit establishment, limit growth, and/or reduce injuriousness of a given pest population. To prohibit establishment and population growth, tactics are aimed at making a pest's effective environment inhospitable . . .

Southwood and Way (1970; p. 6) noted that:

> The basis of the management of a pest is the planned manipulation of the various processes that influence the economic injury level, so as to minimize the economic effect of the pest.

Biologically intensive pest management offers a similar philosophy where alternative methods for managing pests are substituted for chemically-based management (Frisbie *et al.*, 1992). Both of these methods emphasize the use of nonchemical means of managing pests and the prevention of injury to plants by making the ecosystem less favorable for the development of pest outbreaks. For example, Frisbie *et al.* (1992) predicted that a typical cotton IPM program in the year 2012 would: (a) use 20% less pesticides than programs today, (b) rely on resistant varieties and cultural controls to reduce the abundance of pests, and (c) use companion cropping and other nontraditional cropping systems to increase the abundance of beneficial arthropods.

It also will be important to increase farmer participation in the development and testing of IPM programs. Farmer involvement is already occurring in many IPM programs in developing countries. Researchers may fail to understand the importance of how pest management decisions are currently being made by farmers and how their proposed management system alters this process. Rogers (1983) defined several attributes that greatly affect acceptance or rejection of innovative technology: relative advantage over current systems, compatibility with the user's ideas on farm operations, and complexity of the innovation. Stoner *et al.* (1986) noted that the naturalistic philosophical basis and the lack of readily observable advantages slow the acceptance of many IPM programs, so the degree of confidence in a program also must be quantified. This is a major problem with IPM systems because it is easier for farmers to apply an insecticide on a schedule than it is to monitor and manage insect pests with multiple tactics. Therefore, a significant input in the development of new IPM systems must include a component for assessing farmers' needs and for educating them as to why an inherently more complex approach is necessary. Failure to include such components may result in the development of effective IPM systems that are ignored by farmers.

IPM systems based on scouting have several competitive disadvantages over traditional, chemically based methods for managing insect pests without scouting. Wearing (1988) noted that there is a high ratio of pesticide salespersons and distributors to IPM specialists, that farmers have confidence in pesticides, that chemical company personnel have excellent marketing skills, and pesticides are very easy to use. The substitution of labor needed to scout insects for capital investments for chemicals in traditional IPM programs is counter to modern trends in the business world (Wearing, 1988) where labor-saving devices such as dishwashers are economically rewarding substitutes for hand labor. IPM programs developed for use in the future must either eliminate regular scouting or time scouting to periods when attacks of pests are more likely, e.g. via prediction models or pheromone trap captures of adults.

Insect Feeding Guilds

In peanut, insect pests generally occur as a group of mixed species rather than as exclusively one species. The feeding by multiple species of insects on plants led to the grouping of these species into injury guilds based on a plant's physiological response to injury (Smith and Barfield, 1982; Hutchins *et al.*, 1988). Six categories of insect injury were proposed, including (a) stand reduction, (b) leaf-mass consumption, (c) assimilate removal, (d) water balance disruption, (e) fruit destruction, and (f) architecture modification (Hutchins *et al.*, 1988). Categorization of insect injury into a particular group requires homogeneity in both the type of injury and in the plant's response to the injury (Pedigo *et al.*, 1986). Direct injury by foliage feeders on peanut may extend beyond simple leaf-mass removal to fruit destruction via flower and peg feeding (Deitz *et al.*, 1992), and indirect injury through disruption of water balance due to leaf injury (Ostlie and Pedigo, 1984). However, as

long as the type of injury by the group of herbivores is generally equivalent [i.e., it occurs on equivalent plant parts and during equivalent plant physiological stage(s)] the injury can be expressed as an injury-equivalent regardless of the insect species causing the damage. This injury equivalency concept allows development of multiple-species economic injury levels based on injury rather than on injury levels for a single species of insect (Hutchins *et al.*, 1988). Developing economic injury levels for multiple species of insects requires a better understanding of physiological responses of plants to injury by insects (Higley, 1992).

FOLIAR FEEDING GUILD OF INSECTS ATTACKING PEANUT

Foliar Feeding Insects and Plant Injury

The foliar-feeding injury guild of insects which attack peanut is comprised primarily of immatures of the order Lepidoptera. Smith and Barfield (1982) listed 66 species of Lepidoptera that feed on peanut, most of which consume foliage. However, considerable diversity in feeding habits exists even among the foliage feeders. For example, the groundnut leafminer, *Aproaerema modicella* Deventer, feeds internally between the lower and upper leaf epidermis during the first and second instars but emerges during the third instar and webs two or more leaves together, between which it continues to feed and develop (Wightman *et al.*, 1990); the rednecked peanutworm, *Stegasta bosqueella* (Chambers), feeds almost exclusively in developing terminals (Wall and Berberet, 1979); and the corn earworm feeds on developing terminals, young foliage, flowers, and immature pegs (Deitz *et al.*, 1992). Thus, subdivisions in the foliar-feeding guild, e.g. leaf mass removers, terminal feeders, multiple plant part feeders, may be necessary to characterize the type of injury for this diverse group of insects (Simberloff and Dayan, 1991).

Higley (1992) reported that the mechanism of yield reduction in another legume (soybean) due to defoliation by insects is reduced light interception by the defoliated canopy. He noted a significant linear relationship between light interception after insect defoliation and yield that was consistent across locations and between years. In peanut, the upper 42% of the canopy leaf area intercepts 74% of the light and fixes 63% of the CO_2 (Boote *et al.*, 1980). The upper canopy contains younger photosynthetic tissue that is more active in the interception of light and production of photosynthates than is the older, shaded leaves of the mid and lower canopy. Many lepidopterous defoliators prefer to feed on the younger leaves and terminals in the upper canopy (Garner and Lynch, 1981; Pencoe and Lynch, 1982; Deitz *et al.*, 1992). Removal of tissue from the upper canopy by insect feeding reduces CO_2 uptake and the carbon exchange rate (Boote *et al.*, 1980).

Physiological recovery of a plant after defoliation depends on the stage of plant development at the time of injury (Jones *et al.*, 1982). The initial mechanism of physiological recovery by peanut after partial defoliation is the

re-adaptation of older leaves to more efficiently use sunlight, which generally requires 1 to 2 weeks after defoliation of the upper canopy. The second recovery mechanism following defoliation is the production of new leaf tissue. Both recovery mechanisms, especially the production of new leaves, decline late in the growing season when plants are in the pod-set and pod-fill stages of plant development. Defoliation also alters the partitioning of photosynthate between vegetative and reproductive plant parts (Wilkerson *et al.*, 1984). After defoliation, new leaves and vegetative branches are produced which require a higher percentage of the photosynthate, resulting in reduced stem and pod weights, fewer large pods, and reduced expansion of smaller pods (Williams *et al.*, 1976; Wilkerson *et al.*, 1984). Nonuniform defoliation, such as that produced by lepidopterous larvae feeding on terminals and young leaf tissue in the upper canopy, affects partitioning of photosynthate more than uniform leaf removal throughout the peanut canopy (Wilkerson *et al.*, 1984).

Biological Advances for Foliar Feeding Insects

Lepidopterous larvae of the family Noctuidae are the most important defoliators of peanut worldwide and include *Helicoverpa armigera* (Hübner), *H. zea* (Boddie), *Spodoptera frugiperda* J. E. Smith, *S. littoralis* (Boisduval), *S. litura* (Fab.), *Anticarsia gemmatalis* Hübner, and *Agrotis subterranea* (Fab.) (Table 1). *Helicoverpa* spp. and *A. gemmatalis* moths lay their eggs singly and, in the case of *H. zea*, on the underside of leaves in the upper canopy (Pencoe and Lynch, 1982). Newly emerged larvae feed in unexpanded terminals and flowers where they are protected. Older larvae feed openly on

Table 1. Foliage feeding guild of major insect pests of the order Lepidoptera of peanut [modified after Lynch *et al.*, 1986; Wightman *et al.*, 1990; Gahukar, 1992; Lynch and Douce, 1992 (for a more comprehensive list of arthropods that feed on peanut, see Smith and Barfield, 1982)].

Taxon	Common name	Distribution
Amsacta spp.	Hairy caterpillars	Asia, Africa
Anticarsia gemmatalis Hübner	Velvetbean caterpillar	Americas
Aproaerema modicella Deventer	Groundnut leafminer	Asia, S. Africa
Agrotis subterranea (Fabricius)	Granulate cutworm	Americas
Helicoverpa armigera Hübner	Old World bollworm	Asia, Africa
Helicoverpa zea (Boddie)	Corn earworm	Americas
Spodoptera exigua (Hübner)	Beet armyworm	Asia, Africa, Americas
Spodoptera frugiperda (J.E. Smith)	Fall armyworm	Americas
Spodoptera littoralis (Boisduval)	African armyworm	Africa
Spodoptera litura (Fabricius)	Tobacco caterpillar	Asia
Stegasta bosqueella (Chambers)	Rednecked peanutworm	Americas

the plant and show a preference for terminals and young foliage which declines with age of the insect (Deitz *et al.*, 1992). Several of these major defoliators also damage peanut pegs (Deitz *et al.*, 1992). Corn earworm larvae consume 175 to 200 cm^2 of peanut foliage during their development, 75 to 97% of which occurs in the last two instars (Huffman and Smith, 1979).

Spodoptera moths lay their eggs in masses on leaflets, and newly emerged larvae feed on the underside of leaflets, in terminals or behind leaf petioles. Initially, their feeding results in skeletonization of leaflets. Older *Spodoptera* larvae feed on younger leaves and consume about 100 cm^2 of foliage during their development, with more than 80% consumed in the last two instars (Garner and Lynch, 1981). Larvae consume almost twice as much foliage during pod-fill (67 to 92 days after planting) as they do during flowering and pegging (45 to 70 days) (Barfield *et al.*, 1980). Moths originating from larvae that develop during the pod-fill stage are more than twice as fecund as their counterparts that develop during the flowering and pegging stage.

Arctiid larvae of the genus *Amsacta* are among the most devastating defoliators of peanut in India. Their biology has been described by Amin (1988) and Wightman *et al.* (1990). Moths emerge in the field shortly after the first seasonal rain and lay their eggs in clusters on or around plants. Initially they feed *en-masse* on the underside of leaves. As peanuts emerge, larvae move to the plants and feed individually on leaves. Their feeding may result in extensive peanut defoliation in a very short time.

The groundnut leafminer is currently the most serious pest of peanut in Southeast Asia (Amin, 1988; Wightman *et al.*, 1990; Gahukar, 1992; Shanower *et al.*, 1993). Moths deposit their eggs on the underside of leaves or on petioles and stems. First-instars tunnel into the leaflet where they construct serpentine mines as they feed on mesophyll between the upper and lower epidermis. Third-instars leave the mine and web a leaflet or leaflets together, where they feed on leaf tissue and complete their development. A single larva consumes 175 cm^2 of peanut leaf tissue during its development (Islam *et al.*, 1983). During heavy infestations, entire leaflets are mined and die, and severely infested plants may die from the extensive destruction of photosynthetic tissue.

Peanut is most susceptible to yield loss as a result of defoliation by insects during pod initiation and pod fill stages of plant development, approximately 50-90 days after planting (Nickle, 1977; Smith and Barfield, 1982; Wilkerson *et al.*, 1984; Murty *et al.*, 1985). Maximum yield loss from defoliation appears related to the length of the developmental cycle for a particular cultivar. Cultivars with a short growing cycle of 90 to 100 days appear more susceptible at approximately 50 to 70 days after planting (Murty *et al.*, 1985), while cultivars with a long growing cycle are more susceptible at approximately 70 to 90 days after planting (Nickle, 1977; Smith and Barfield, 1982). Davis and Mack (1991) reported that most peanut growth characteristics increase linearly with time and developed equations to predict leaf area index from dry leaf weight, number of leaves, plant height and plant vegetative stage. The yield loss data reported by Nickle (1977) was used to develop linear regression equations for yield loss by plant growth stage (T.P. Mack and D.

Table 2. Regression equations for yield loss in peanut due to defoliation by foliage-feeding insects at different stages of peanut development [regression equations developed by T. P. Mack and D. P. Davis (unpubl. data, 1993) from data reported by Nickle (1977)].

Plant stage	Regression equation[a]	R^2
Early vegetative	Y = 105.8 - 0.42x	0.89
Flowering	Y = 105.9 - 0.66x	0.96
Pegging	Y = 97.0 - 0.68x	0.98
Pod fill	Y = 106.6 - 0.75x	0.94
Maturation	Y = 102.1 - 0.23x	0.84

[a]Y = % of maximum yield; x = % defoliation.

P. Davis, unpubl. data, 1993) which showed that defoliation is most critical in the pegging and pod fill stages (Table 2). Defoliation had minimal effects in early vegetative stages or during pod maturation, similar to that reported by Smith and Barfield (1982). A defoliation model based on these data is presently being validated in the field.

Biological Control

Very little is known about beneficial arthropods in peanut fields. The spider complex was studied in the southwestern U.S. by Agnew *et al.* (1985) and Agnew and Smith (1989). They noted that most of the colonizing species were hunting spiders, with the families Oxyopidae, Lycosidae, and Thomisidae dominating. Lycosids were more abundant in closed canopy fields that were irrigated than they were in open canopy, rain-fed fields. The importance of generalist predators in peanut fields is sometimes overlooked. Agnew and Smith (1989; p. 41) summarized the importance of all generalist predators by stating for spiders:

> Spiders attack a large range of pest species, they prey throughout all stages of their development, they are relatively long-lived, they colonize fields early and rapidly, they are resistant to starvation and desiccation, and they do not emigrate in large numbers during periods of low prey density.

More studies are needed on generalist predators, particularly microarthropod predators in peanut fields. Predaceous mites and predaceous collembolans are common in some peanut fields (A. Mabrouk and T.P. Mack, unpubl. data, 1993), but their contribution to overall mortality of peanut insects is currently unknown. Increased efforts are needed to quantify the importance of generalist predators and to either maintain or augment their abundance.

Each species of defoliating insect has a variety of natural enemies which attack different stages during the insect's development. References for the natural enemies for most of the lepidopterous defoliators are listed in Smith and Barfield (1982). Natural enemies of the groundnut leafminer are discussed by Amin (1988) and Shanower *et al.* (1992). An illustration of the diversity in natural enemies of defoliators is presented using the corn

Table 3. Major natural enemies of *Helicoverpa zea* in the southern U.S. (modified after Nordlund *et al.*, 1986; Kharboutli and Mack, 1991).

	Stage of *Helicoverpa* attacked				
		Larval instars			
Group/order/taxon	Egg	1-2	3	4-5	Pupa
Predators					
Hymenoptera					
Solenopsis invicta Buren	x	x	x		
Hemiptera					
Geocoris punctipes (Say)	x	x			
Nabis spp.	x	x	x		
Orius insidiosus (Say)	x	x			
Dermaptera					
Labidura riparia (Pallas)	x	x			
Neuroptera					
Chrysoperla spp.	x	x	x		
Chrysopa spp.	x	x	x		
Coleoptera					
Hippodamia convergens Guérin-Méneville	x	x			
Coleomegilla maculata (DeGeer)	x	x			
Calosòma spp.		x	x	x	x
Natoxas spp.		x	x		
Araneida					
Spiders		x	x	x	x
Parasitoids					
Hymenoptera					
Cardiochiles nigriceps (Vierick)		x	x	x	
Chelonus insularis (Cresson)	x	x[a]	x[a]	x[a]	
Cotesia marginiventris (Cresson)		x			
Campoletis spp.		x	x		
Trichogramma spp.	x				
Diptera					
Archytas marmoratus (Townsend)		x	x	x	x[b]
Lespesia spp.		x	x	x	
Eucelatoria bryani Sabrosky		x	x	x	
Pathogens					
Viruses					
Ascovirus		x	x		
Nuclear polyhedrosis virus		x	x	x	
Bacteria					
Bacillus thuringiensis Berliner		x	x	x	
Fungi					
Beauveria bassiana (Bal.) Vuillemin		x	x	x	x
Nomuraea rileyi (Farlow) Samson		x	x	x	
Entomophthora spp.		x	x	x	
Microsporidia					
Nosema heliothidis Lutz and Splendor	x	x	x	x	x

[a]Parasitizes eggs, but completes development in the larva.

[b]Parasitizes larva, but may complete development in the pupa.

earworm as an example (Table 3). Several species of generalist predators such as earwigs, big-eyed bugs, fire ants, nabids, lady beetles, carabids, and spiders (Agnew and Smith, 1989; Kharboutli and Mack, 1991, 1993) feed on eggs and larvae of the corn earworm. Likewise, several species of hymenopterous parasites, primarily braconid wasps and tachinid flies, play important roles in reducing populations of this insect. Pathogens also are major components in the biological control of the corn earworm. In particular, the nuclear polyhedrosis virus often decimates populations of *H. zea* if the disease epizootic is allowed to proceed naturally (Sears and Smith, 1975; R.E. Lynch, pers. obs.), and defoliation by this insect in subsequent generations within the remainder of a growing season is minimal. A more comprehensive review of the potential for management of *Helicoverpa* with natural enemies is presented by King and Coleman (1989) and Sterling (1989).

Pheromones

Sex pheromones have been identified for a number of the more important lepidopterous defoliators of peanut. Several of the pheromones have been used to monitor adult male populations as indices of population density over time (Lynch and Douce, 1992). Probably the most extensive research with pheromone of peanut pests has been with *S. litura* in India. Positive correlations were reported between the number of *S. litura* egg masses found on peanut and the total number of male moths captured in pheromone traps during the 7 days immediately preceding the field survey for egg masses (Sridhar *et al.*, 1988). This pheromone trapping program in India has since been standardized and is now used in a national monitoring program for *S. litura* (Ranga Rao *et al.*, 1991).

Host Plant Resistance

Resistance to leaf-feeding has been reported for several major defoliators of peanut (Lynch, 1990). In particular, the breeding lines NC Ac 342 and GP-NC 343, and the cultivars NC 6 and Early Bunch have moderate levels of antibiosis to the corn earworm (Campbell and Wynne, 1980; Campbell *et al.*, 1982). Todd *et al.* (1991) evaluated eight peanut cultivars for resistance to the corn earworm, fall armyworm, and velvetbean caterpillar and found that NC 6 and Tifton 8 were the most resistant. Resistance to *S. litura* has been reported in ICGV 86031 where more than 1/2 of the first instars fail to become established in laboratory studies, and only 29% of the larvae survived to become adults (Wightman *et al.*, 1990). Resistance to the groundnut leafminer has been reported in the cultivar M 13, and in breeding lines GP-NC 343, ICG 7758, ICG 8322, ICG 10361, and ICG 9219 (Gahukar, 1992). Wightman and Amin (1988) reported that 33 peanut accessions have been confirmed with resistance to the groundnut leafminer at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in India.

High levels of resistance to insect defoliation, often approaching immunity, have been reported in wild species of *Arachis* (for review, see Lynch, 1990). Lynch *et al.* (1981) reported resistance to *S. frugiperda*, Stalker and Campbell (1983) reported resistance to *H. zea*, and J. A. Wightman and P. W. Amin

(pers. commun., 1993) reported resistance to the groundnut leafminer and *S. litura*.

Recently, Stevenson *et al.* (1993b) evaluated 14 wild species of *Arachis* for resistance to *S. litura*, all were resistant compared to the susceptible TMV 2. Mortality of neonates exposed to excised leaves of *A. batizogaea*, *A. kempff-mercadoi*, *A. appressipila*, *A. paraguariensis*, *A. stenophylla*, and *A. villosa* exceeded 90% compared with less than 20% on TMV 2. Using a penetrometer, leaves of most of the wild species were tougher than leaves of TMV 2 resulting in a negative correlation between toughness and larval development. Chemical analyses of leaves of *A. paraguarensis*, *A. diogoi* (formerly *A. chacoensis*), and the hybrid *A. diogoi* (formerly *A. chacoensis*) x *A. hypogaea* showed the presence of quercetin diglycocides and caffeoylquinic acids (Stevenson, 1993). Further analyses of the caffeoylquinic acids in *A. paraguarensis* showed that 1-caffeoyl-4-deoxyquinic acid (1-CdQA), 3-caffeoylquinic acid (3-CQA), and 5-caffeoylquinic acid (5-CQA = chlorogenic acid) (Stevenson *et al.*, 1993a). Development of *S. litura* larvae fed diets treated with 1-CdQA, 3-CQA, and 5-CQA was severely inhibited compared with larvae fed untreated diet.

SOIL-INHABITING GUILD OF ARTHROPODS ATTACKING PEANUT

Soil-Inhabiting Arthropods and Plant Injury

Soil insects are key pests of peanut worldwide. The lesser cornstalk borer, *Elasmopalpus lignosellus* (Zeller) (Insecta: Lepidoptera: Pyralidae), is a key pest of peanut in the southeastern U.S. and a complex of termites (*Odontotermes* spp. and *Microtermes* spp.) and white grubs (*Lachnosterna* spp.) limit yields of peanut in semi-arid Africa. Smith and Barfield (1982) noted that soil insect pests pose several special problems. First, sampling for soil insects is often time-consuming, destructive, and laborious. Sampling is something pest management consultants would probably like to avoid. Secondly, damage from soil insects is usually below-ground and hard to discern, so one cannot determine yield loss from an easily measurable above-ground variable such as percentage defoliation. A third problem is that important aspects of the biology, ecology, and especially the biotic and abiotic interactions of soil insects are not well understood. This greatly complicates the development of management systems for soil insects.

How do plants respond to injury from soil insects? Damage by soil insects not only affect the roots and pods, but may affect the entire plant. General plant responses to root- or stem-feeding injury include stunting, decreased leaf area production, diminished root, pod, and/or seed dry weight, reduced xylem sap pressure, a decline in photosynthate flow in phloem tissues, and decreased nitrogen-fixing activity (Powell and Campbell, 1983; Mack *et al.*, 1988a). In addition to feeding on the roots and tunneling in the tap root and/or lateral branches, soil insects also damage peanut by feeding on developing pegs, feeding externally on pods, or by penetrating the pods and feeding on

developing seed. Stunting and wilting of plants attacked by stem- or root-feeding insects are common symptoms of stem or root damage, strongly suggesting a decline in water transport within the plant (Wightman *et al.*, 1990). Insects, such as the lesser cornstalk borer, termites, and white grubs, often sever or tunnel in the tap root or feed on roots, disrupting water absorption and/or transport in peanut plants. Lack of sufficient water to meet the demands of stems and leaves because of damage by these insects to xylem tissue results in plant stress and wilting. Likewise, destruction of phloem tissue inhibits translocation of assimilates to meet the demands for root growth. Wound-healing mechanisms include the production of adventitious roots and partial to complete "scabbing-over" of damage sites.

Biological Advances for Soil-inhabiting Arthropods

Peanut is attacked by several species of arthropods that are epigaeic or subterranean (Table 4). Soil-inhabiting insects are usually key pests of peanut worldwide because they often damage the harvestable product. In the U.S., wireworms (*Conoderus* spp.) and southern corn rootworm (*Diabrotica undecimpunctata howardi* Barber) damage to peanut is greater during periods when soil water is adequate and populations of these pests increase. In contrast, lesser cornstalk borer population survival is greater during periods of drought and damage is greater during these periods. In Africa and Asia, several species of white grubs, termites, the groundnut hopper (*Hilda patruelis* Stal.), the oriental army ant (*Dorylus orientalis* Westwood), and millipedes (*Peridontopyge* spp.) cause extensive damage to peanut under a wide variety of edaphic conditions (Demange, 1975; Amin, 1988; Wightman *et al.*, 1990; Gahukar, 1992; Van Eeden *et al.*, 1993).

White Grubs. Smith and Barfield (1982) listed 26 species of white grubs (Scarabidae) that attack peanut worldwide. Wightman *et al.* (1990) expanded the list by adding five new genera and up to 30 new species of scarabs that damage peanut. The white, c-shaped grubs of scarabs are considered among the most important insects that attack peanut in the developing nations of Africa and Southeast Asia (J. A. Wightman, pers. commun., 1993) and may produce yield losses exceeding 40% (Bakhetia, 1983). Recent research in South Africa also demonstrated the importance of this group of insects on peanut (Van Eeden *et al.*, 1993). A general description of the biology of white grubs and their damage to peanut was reported by Amin (1988), Wightman *et al.* (1990), and Gahukar (1992). Several species of the genera *Adoretus, Anomala, Eulepida, Lachnosterna*, and *Schizonycha* feed on peanut roots and pods in Southeast Asia and Africa. Adults emerge from the soil at the onset of the rainy season, feed on wild hosts, and mate. Eggs are laid singly or in small clusters approximately 5 to 15 cm below the soil surface. White grubs complete three larval instars: the early instars feed on plant rootlets and nodules and later instars feed on the tap root or pods and often devour the entire tap root. This severe damage to the tap root by the late instar grubs results in isolated patches of dead plants in peanut fields. White grubs are most damaging in sandy soil or well-tilled loamy soils, especially when rainfall is above average.

Table 4. Soil-inhabiting guild of major arthropod pests of peanut [modified after Lynch *et al.*, 1986; Wightman *et al.*, 1990; Gahukar, 1992; and Lynch and Douce, 1992 (for a more comprehensive list of arthropods that feed on peanut, see Smith and Barfield, 1982)].

Group/taxon	Common name	Distribution
White Grubs		
Eulepida mashona Arrow		Africa
Lachnosterna consanguinea Blanchard		Asia
Lachnosterna serrata Fabricius		Asia
Buprestid		
Sphenoptera indica (Guer.)	Jewel beetle	Asia
Rootworm		
Diabrotica undecimpunctata howardi Barber	Southern corn rootworm	Americas
Wireworms		
Conoderus spp.		Americas
Lepidoptera		
Elasmopalpus lignosellus (Zeller)	Lesser cornstalk borer	Americas
Termites		
Microtermes spp.		Africa, Asia
Odontotermes spp.		Africa, Asia
Tettigometrid		
Hilda patruelis Stål	Groundnut hopper	Southern Africa
Ants		
Dorylus orientalis Westwood	Oriental army ant	Asia
Earwigs		
Anisolabis annulipes (Lucas)	Ring-legged earwig	Asia
Diplopoda		
Peridontopyge spp.	Millipedes	Africa

a. Biological control. Brar and Sandhu (1980) listed the natural enemies of white grubs in India. These include several species of birds and toads; the fungi *Beauveria bassiana* (Bal.) Vuillemin and *Metarrhizium anisopliae* var. *anisopliae* Met. and Sorok; the bacteria *Bacillus thuringiensis* and *B. popilliae* var. *holotrichiae* Milner (Vyas *et al.*, 1986); carabid beetles; and two scolid parasitoids, *Scolia aureipennis* Lep. and *Campsomeris callaris* (Fab.).

b. Host plant resistance. Plant resistance in peanut to white grub is presently a high priority at ICRISAT (J. A. Wightman, pers. commun., 1993). Although resistance to white grubs has not been reported, resistance in the wild species of *Arachis* to a related coleopteran species, the jewell beetle [*Sphenoptera indica* (Guer.)], has recently been identified (J. A. Wightman, G. V. Ranga Rao, and J. P. Moss, pers. commun., 1993).

Termites. Several species of termites have been reported to damage peanut (Wightman *et al.*, 1990) with species of the genera *Odontotermes* and *Microtermes* as major pests in Southeast Asia and Africa (Johnson *et al.*, 1981; Lynch *et al.* 1986; Wightman and Amin, 1988). Species of *Odontotermes* may cover much of the plant with soil and feed on the leaves, but the greatest damage is caused by feeding on pods or tunneling in the tap root, main stem, and/or lateral branches (Johnson *et al.*, 1981; Wightman *et al.*, 1990). Pod damage by termites is characterized by removal of the exocarp without pod penetration—i.e., scarification—or by pod penetration where the insects feed on the seed (Amin, 1988; Lynch *et al.*, 1990). Damage by termites reduces yield and decreases quality because of increased invasion by *Aspergillus flavus* Link and subsequent aflatoxin formation (Lynch *et al.*, 1990, 1991; Lynch and Douce, 1992).

Termite damage to peanut is greater during insufficient rainfall, especially during the latter part of the growing season (Johnson *et al.*, 1981). A significant linear relationship has been shown between tap root invasion by termites and soil moisture (Johnson *et al.*, 1981). Yield losses due to termite damage may exceed 40%, with over 80% pod scarification among plants having their tap root invaded (Johnson *et al.*, 1981). Damage to peanut by termites also is enhanced by irregular plant maturity and a delay in harvest at the end of the rainy season (Lynch *et al.*, 1990, 1991).

a. Biological and cultural control. Little research has been conducted on the natural enemies of termites in peanut. Wightman *et al.* (1990) reported that termites are natural prey for ants, and that birds, rodents, bats and other insectivorous vertebrates often are observed feeding on termites.

Cultural methods have been the primary means for managing termite damage to peanut in the developing nations and include planting high quality seed that result in a more uniform plant stand; planting cultivars of the appropriate maturity cycle for a given location, harvesting early before the decline in soil moisture reaches a level conducive to termite damage, and deep ploughing and cultivating to destroy termite tunnels and reduce populations of this insect.

b. Host plant resistance. Plant resistance to pod scarification and penetration by termites was reported by Amin *et al.* (1985) in GP-NC 343, NC Ac 2232, NC Ac 2242, NC Ac 2243, and NC Ac 10033 in India. Resistance in these lines also was evaluated and confirmed in Burkina Faso, West Africa, and additional cultivars—RMP 40, RMP 12 and Bonga—were identified as resistant to both plant and pod damage (Lynch *et al.*, 1990; Dicko *et al.*, 1991; Ouédraogo *et al.*, 1993).

Lesser Cornstalk Borer. The most commonly studied soil insect in U.S. peanut is the lesser cornstalk borer, and several accounts of the damage to peanut have been published (Berberet *et al.*, 1979a; Smith and Barfield, 1982). Small larvae feed on vegetative buds, leaves, and plant stems primarily at the ground level. Larger larvae feed on the stem and taproot at the root-hypocotyl region (Mack *et al.*, 1988b, 1990) and on pegs and pods (Lynch, 1984).

Most of the studies on soil insects have concentrated on relating damage

from the lesser cornstalk borer to yield. Smith and Holloway (1979) reported that 28- to 58-day-old spanish peanut may be more severely injured by larval feeding on young flower buds concentrated in the plant crown before gynophore and pod formation. They also showed that yields decreased in a curvilinear manner with increasing density of lesser cornstalk borer larvae. Berberet *et al.* (1979a) found that yield declined linearly at 60-110 days after planting from lesser cornstalk borer larval injury to peanut.

The studies by Smith and Holloway (1979) and Berberet *et al.* (1979a) were field trials. Mack *et al.* (1988b) reported on the results of a greenhouse test, where Florunner peanut at one of five plant phenologies was artificially infested with one of five densities of small larvae of the lesser cornstalk borer. They found that uninjured pod, seed, and root dry weight declined linearly with an increase in density of lesser cornstalk borer larvae. Larvae do not directly feed on root tissues. Mack *et al.* (1988b) also found that dry weight of undamaged seeds declined linearly with an increase in density of lesser cornstalk borers, even when larvae completed development before pods were formed.

Damage by the lesser cornstalk borer, like other soil insects, may affect the entire plant. Mack *et al.* (1990) investigated larval injury to Florunner, and found that lesser cornstalk borer larvae cause significant injury to the periderm, cortex, and phloem in the root-hypocotyl region of peanut. About 32% of the periderm and cortex, 17% of the phloem, and <1% of the xylem was directly removed by larval feeding in this region. Feeding injury of this type should have affected nutrient transport to roots and possibly reduced turgor pressure because of injury to the outer cells of the xylem. Both exposed xylem and other cells many layers deep typically died from the loss of protective tissues. A reduction in turgor pressure and a decline in photosynthate flow to roots would explain why peanut plants severely injured by lesser cornstalk borers are often wilted.

Wound depth is an indicator of the physiological impact of insect feeding to stems or taproots (Powell and Campbell, 1983), with greater depth indicating greater injury. These results, when coupled with the previous studies, show that lesser cornstalk borer injury to the root-hypocotyl region is a physiologically-damaging stress that affects the entire plant and not just seed production (Fig. 2).

Two studies report economic injury levels for the lesser cornstalk borer in peanut. Smith and Holloway (1979) related larval injury to yield in conventionally planted and tilled spanish peanut. Mack *et al.* (1988b) reported an economic injury level of 3.6 to 5.4 larvae per m/row for conventionally planted and tilled Florunner plants. No studies have examined yield-loss relationships in reduced tillage or narrow row planting.

Lesser cornstalk borer injury to the root-hypocotyl region includes the removal of periderm (Mack *et al.*, 1990). This tissue can act as a deterrent to fungal penetration and colonization, so the removal of periderm would predispose plants to attack by pathogens such as whitemold, *Sclerotium rolfsii* Sacc. Open wounds with tissue removed down to the xylem should be much more susceptible to attack by fungal penetration and colonization than

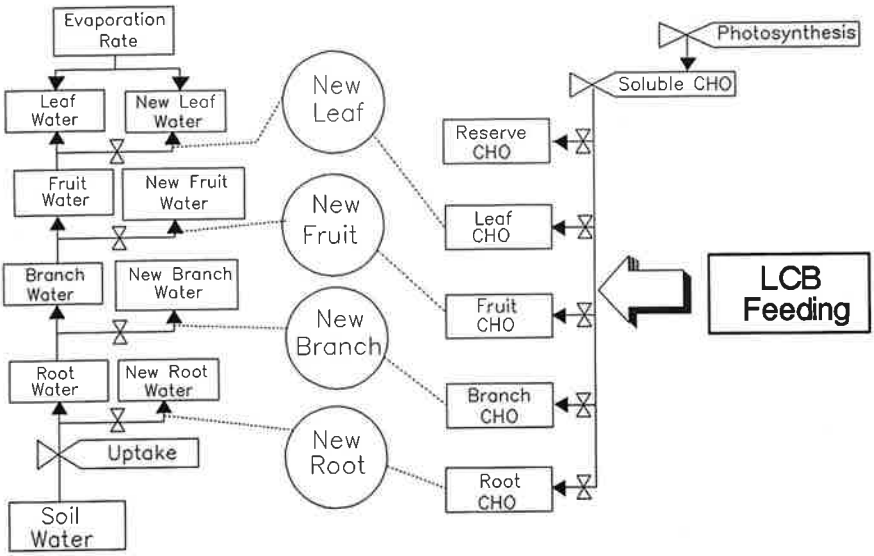

Fig. 2. Effects of lesser cornstalk borer larval feeding on peanut plant growth. CHO represents carbohydrate and LCB is the lesser cornstalk borer.

tissues with an intact periderm. No published studies confirm or deny this hypothesis. However, chlorpyrifos, is the most effective insecticide registered for use against the lesser cornstalk borer (Mack *et al.*, 1991b) and is also registered for suppression of whitemold.

Lesser cornstalk borer larvae feed directly on pegs and pods. Larvae can severely damage young pods but are unable to penetrate older pods once structural rigidity of the mesocarp was established (Lynch, 1984). Older pods become externally scarified; this is characterized by the removal of external pod tissue without complete penetration of the pod. Injury of this type to pods is associated with development of aflatoxigenic fungi in peanut (Sanders *et al.*, 1985; Lynch and Wilson, 1991) but, until recently, no studies have shown that the lesser cornstalk borer transmits *A. flavus* propagules to peanut pods in the field. Lynch and Wilson (1991) also showed that lesser cornstalk borer larvae were excellent vectors of *A. parasiticus* to all developmental stages of peanut pods and that over 50% of lesser cornstalk borer larvae collected in the field were contaminated with propagules of *A. flavus*-type fungi. Larvae passively carry fungal propagules on their cuticles. They also noted that the percentage of *A. flavus*-type fungi increased when amount of injury to pods increased from the lesser cornstalk borer. Bowen and Mack (1993) reported similar results, and also found that 8.9% of surface-sterilized, macerated larvae yielded living propagules of *A. flavus*, so fungal propagules must be in the larval gut.

These findings have important implications for management of the lesser cornstalk borer. Economic injury levels need to be revised with consideration

for disease augmentation as a result of insect damage. Currently, growers use one application of an insecticide during the growing season for the lesser cornstalk borer as needed. In outbreak years, two applications of an insecticide might be required because none of the current insecticides provide enough residual control to protect the plant from blossoming until harvest (Mack *et al.*, 1991b). One of these applications would probably be applied at flowering time and a second application later in the season. Currently, no state extension programs recommend two applications of a granular insecticide, so further study is needed.

Late infestations of lesser cornstalk borer larvae may pose another problem if they occur after the harvest interval time has expired for the currently registered insecticides. Infestations sometimes occur in peanut just before harvest. Late infestations such as this could be controlled with an application of *B. thuringiensis*, which has been shown to be effective against the lesser cornstalk borer (W. J. Moar and T.P. Mack, unpubl. data, 1993). However, *B. thuringiensis* may not be able to survive the harsh microclimate of the soil surface for more than 48 hours.

Management of soil insects typically relies on prevention of population outbreaks from occurring because of the difficulty in sampling. Management of the lesser cornstalk borer in the early 1980s traditionally followed this path (Smith and Barfield, 1982). A more thorough understanding of the biology and ecology of this insect in relationship to its environment, peanut plants, and arthropod natural enemies would encourage the development of management practices targeted at weak points in the insect's life cycle.

a. Biology and ecology. Huang and Mack (1989) and Huang *et al.* (1990) studied the olfactory responses of lesser cornstalk borer larvae to peanut plant parts with the idea of identifying volatile attractants and nonvolatile phagostimulants for larvae. Their idea, as yet undeveloped, is to produce an attractive bait formulation for use against larvae. Larvae are known to crawl on the soil surface because they are captured in pitfall traps (Mack, 1992).

As detailed in Smith and Barfield (1982), population outbreaks of the lesser cornstalk borer typically occur during hot and dry weather when peanut is grown in sandy soils. Abiotic factors, then, play a critical role in development of outbreaks. There are several factors that contribute to this. Berberet *et al.* (1982) and Mack and Backman (1984, 1986, 1987) studied the effects of constant and fluctuating diel temperatures on the oviposition rate of the lesser cornstalk borer and concluded that high maximum daily temperatures contribute to the development of population outbreaks by increasing the daily oviposition rate and the total number of eggs laid/female. Mack and Backman (1987) also studied the life cycle of this insect in the field and monitored all stages of the insect's life cycle weekly for three growing seasons. They found that the growth curves differed in latent and outbreak years, with population growth in outbreak years characterized by exponential growth during hot and dry weather. Growth in latent years did not follow an exponential growth curve. Little immigration was measured in outbreak years. Age structure of adult moths was extremely variable from week to week in both latent and outbreak years. A mathematical model of the lesser

cornstalk borer was developed (Mack *et al.*, 1987), which showed that the increased larval abundance in hot and dry weather was caused by three factors: (a) increased daily oviposition rate, (b) increased rate of development for all stages resulting from higher than normal daily soil temperatures, and (c) decreased egg/larval mortality. These researchers also noted that abiotic factors such as high temperatures and low soil moisture caused major changes to occur in lesser cornstalk borer populations over time. For example, the net reproductive rate of this insect is approximately 1.0 at a constant 21 C, whereas it approaches 7.0 at 30 C. Maximum daily temperatures of >47 C have been measured 2.5 cm under the peanut canopy, so an average of 30 C is achievable in hot and dry weather.

The lesser cornstalk borer is a classical example of "Survival of the Fittest." Its maximum feeding rate on artificial diet occurred at a constant 40 C in a controlled temperature study (V. Borek and T.P. Mack, unpubl. data, 1994). The insect creates a more favorable environment for itself by feeding on the root-hypocotyl region and increasing the likelihood of wilting. This increases the soil temperatures which accelerate larval development.

An explanation as to why mortality of the lesser cornstalk borer decreases in hot and dry weather has been offered by Mack and Appel (1986), Mack *et al.* (1988b), and Appel *et al.* (1991). These studies examined the water relations of the lesser cornstalk borer and several arthropod natural enemies of this insect. Mack *et al.* (1988b) found that the lesser cornstalk borer was a xeric-adapted insect that had a degree of cuticular waterproofing that was similar to a desert scorpion's waterproofing, so it can survive hot and dry weather without significant water loss. However, this is not true for several natural enemies; for example, 100% of red imported fire ants died when exposed to the same desiccating environment (Appel *et al.*, 1991).

Smith and Johnson (1989) developed partial ecological life tables for the lesser cornstalk borer, with unexplained mortality of large larvae being the key factor. Most of the mortality was density independent, implying that abiotic factors were the driving variable in causing population outbreaks. Heat- and water-stressed insects usually respond to these stresses by relocating to avoid the stress, if possible, and by reducing their general level of activity. For example, predators such as red imported fire ants might cease foraging between crop rows and may only forage under rows. During droughts, the peanut plants become water stressed and their leaflets close during the day. This increases penetration of sunlight to the soil surface, thereby causing soil surface temperatures to rise greatly. This probably curtails predator activity. Management practices that would promote the abundance of naturally occurring predators and parasites could reduce the likelihood of outbreaks of hot and dry weather pests such as the lesser cornstalk borer.

b. Biological control. A general survey of arthropod predators in peanut fields in Alabama found that striped earwigs and red imported fire ants were the two most abundant predators (Kharboutli and Mack, 1991). The most abundant arthropod predator is probably the striped earwig, *Labidura riparia* (Pallas) (Kharboutli and Mack, 1991), but this insect cannot tolerate the heat of a xeric environment, as witnessed by its mesic critical thermal

maxima and upper lethal limits (Mack *et al.*, 1988a; Kharboutli and Mack, 1993). It requires free moisture to successfully reproduce (Schlinger *et al.*, 1959), and its abundance appears to decline in hot and dry weather (Mack 1992). Many other researchers have studied the natural enemy complex of the lesser cornstalk borer (Table 5). Carrola (1984) studied the effects of abiotic factors on effectiveness of *Geocoris punctipes* (Say) predation on larvae of the lesser cornstalk borer, and concluded that fewer larvae were likely to be consumed in hot and dry conditions. Several other species of parasitic insects attack the lesser cornstalk borer, including *Orgilus elasmopalpi* Meusebeck, *Pristomerus spinator* (Fab.), and *Stomatomyia floridensis* Townsend. Funderburk *et al.* (1984a) reported that *O. elasmopalpi*, *P. spinator*, and *Chelonus elasmopalpi* McComb were widespread in peanut fields in northern Florida, while Smith and Johnson (1989) noted that six species of parasites caused discernible mortality—*O. elasmopalpi*, *P. spinator*, *C. elasmopalpi*, *Illidops terrestris* Wharton, *Invreia deceptor* Grissel and Schauff, and *Geron aridus* Painter.

Funderburk *et al.* (1984a) reported on a granulosis virus, the entomophagous fungus *Beauvaria* spp., and microsporidia as pathogens of this insect. Mitchell and Smith (1985) identified an entomopox virus that was effective against the lesser cornstalk borer. Studies are underway in Georgia (M. Adang, pers. commun., 1993) and Alabama (W. J. Moar and T.P. Mack, unpubl. data, 1994) to identify genes of *B. thuringiensis* that code for toxins active against the lesser cornstalk borer. Once identified, these genes could be incorporated into the genome of the plant, inserted into an endophyte, or put into a geocarposphere-inhabiting bacterium.

c. Preventive pest management. Tactics that delay the onset of hot and dry conditions of the top 2.5 to 5 cm of soil under the peanut canopy may reduce the probability of an outbreak of the lesser cornstalk borer. This suggests that we could decrease the likelihood of outbreaks by altering microclimate. For example, we found fewer lesser cornstalk borers in peanut planted in mid-May than in peanut planted in early June (Mack and Backman, 1990), probably because wetter conditions in May enabled plant canopies between rows to close faster than in plots planted in June. Maximum daily soil temperatures and evapotranspiration are much less in closed canopy fields because sunlight does not penetrate to the soil surface. This retards development of lesser cornstalk borers.

Closed canopy fields also favor development of striped earwigs. These predators may survive hot and dry conditions in peanut fields by burrowing deeper into the soil and by reducing the length of time they are active during the day. High temperatures also increase movement of the striped earwig and hence body water loss, suggesting limited survival of earwigs in extended droughts. We hypothesize that a management practice that reduces maximum daily soil temperatures and increases soil moisture, such as use of narrow rows or reduced-tillage peanut, should make the microclimate more hospitable for the development of natural enemies and decrease the likelihood of outbreaks from the lesser cornstalk borer.

d. Sampling and predicting outbreaks. Progress has been made in

Table 5. Natural enemies of the lesser cornstalk borer, *Elasmopalpus lignosellus* (Zeller).

Group/taxon	Stage attacked	Reference
Parasites		
Orgilus elasmopalpi Muesenbeck	Larvae	Wall and Berberet (1975) Johnson and Smith (1981) Funderburk *et al.* (1984b) Smith and Johnson (1989)
Orgilus nitidus Muesenbeck	Larvae	Johnson and Smith (1981)
Pristomerus spinator (Fabricius)	Larvae	Wall and Berberet (1975) Berberet *et al.* (1979b) Johnson and Smith (1981) Funderburk *et al.* (1984b) Smith and Johnson (1989)
Chelonus elasmopalpi McComb	Eggs, larvae	Johnson and Smith (1981) Funderburk *et al.* (1984b) Smith and Johnson (1989)
Stomatomyia floridensis Townsend	Larvae	Leuck and Dupree (1965) Wall and Berberet (1975) Johnson and Smith (1981) Funderburk *et al.* (1984b)
Apanteles sp.	Larvae	Wall and Berberet (1975) Berberet *et al.* (1979b) Johnson and Smith (1981)
Bracon gelechiae Ashmead	Larvae	Berberet *et al.* (1979b)
Illidops terrestris Wharton	Larvae	Smith and Johnson (1989)
Macrocentrus sp.	Larvae	Johnson and Smith (1981)
Geron aridus Painter	Pupae	Johnson and Smith (1981) Smith and Johnson (1989)
Invreia deceptor Grissell and Schauff	Pupae	Berberet *et al.* (1979b) Johnson and Smith (1981)
Predators		
Geocoris spp.	Eggs, larvae	Smith and Johnson (1989) Kharboutli and Mack (1991)
Solenopsis invicta Buren	Eggs, larvae	Kharboutli and Mack (1991)
Labidura riparia (Pallas)	Larvae	Kharboutli and Mack (1991)
Philophaga viridicolis LeConte	Larvae, pupae	Smith and Johnson (1989)
Litolinga acuta (Adams)	Larvae	Smith and Johnson (1989)
Cyclotelus rufiventris (Loew)	Larvae	Smith and Johnson (1989)
Spiders	Larvae, adults	Agnew and Smith (1989) Kharboutli and Mack (1991)
Pathogens		
Granulosis virus	Larvae	Funderburk *et al.* (1984b)
Entomopox virus	Larvae	Mitchell and Smith (1985)
Beauveria sp.	Larvae	Funderburk *et al.* (1984b)
Microsporidia	Eggs, larvae, adults	Funderburk *et al.* (1984b)

sampling techniques and spatial distributions of the lesser cornstalk borer. Moth populations were randomly distributed or slightly aggregated in pheromone trap captures (Funderburk *et al.*, 1987). Two recent studies have provided algorithms to predict outbreaks before economic damage occurs. One method uses estimates of adult abundance to predict the abundance of larvae 1 week later (Mack *et al.*, 1991a). This method is currently untested on a large scale. A more promising approach has been recently offered by Mack *et al.* (1993). The authors have developed a concept called borer-days, or LCB Days, which is a running total of the weather events since planting in a given peanut field:

$$Y = (H - W), \qquad \text{Eq. (1)}$$

where Y is LCB Days and represents the cumulative effect of weather on larval abundance, H is the number of days where the temperature was $\geq$35 C and <2.54 mm of rainfall occurred, and W is the number of days that the temperature was <35 C and $\geq$2.54 mm of rainfall occurred. The variable H represents hot and dry days that contribute to population outbreaks of the lesser cornstalk borer, and W is cooler and wetter days that maintain a latent population. H and W are mutually exclusive variables. Neutral days (e.g., $\geq$35 C and $\geq$2.54 mm precipitation) do not contribute to LCB Days.

LCB Days is used to time scouting so that it occurs when larvae are most likely to be present in a field. LCB Days will be positive if many hot and dry days occur, such as during a drought, and negative if rainy weather prevails (Fig. 3). Mack *et al.* (1993) compared the cumulative number of LCB Days in 1986 with densities of lesser cornstalk borer larvae to determine if density increased with LCB Days and explained the variation in densities ($r^2 = 0.67$) during the 1986 outbreak (Fig. 4). They also found that LCB Days were an excellent indicator of population outbreaks of the lesser cornstalk borer. Outbreaks of this insect were accurately predicted from 9 year's data by calculating the number of days after planting in a growing season where $\geq$10 LCB Days were accumulated. Field tests in 1989 and 1990 showed that use

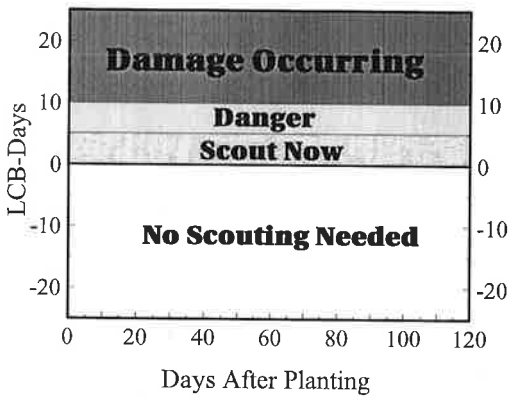

Fig. 3. Four-tiered graphical approach for use of LCB Days to time scouting for lesser cornstalk borer larvae in conventionally planted and tilled peanut fields, planted in sandy loam soils.

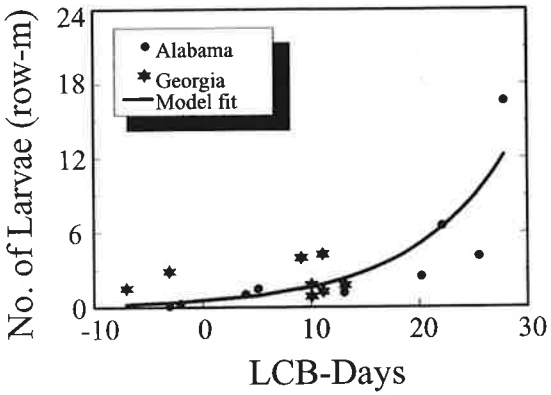

Fig. 4. Lesser cornstalk borer density versus LCB Days for the 1986 epidemic in Alabama and Georgia. The line is from an exponential model fit by nonlinear regression: $Y = 0.5217 * e^{(0.1133 * X)}$, where Y is larval density per soil sieve and X is LCB Days. Each point represents a mean of 10 sieve samples.

of LCB Days correctly predicted the need for scouting in four field tests. LCB Days should help growers to scout fields only when this insect poses a threat. No scouting should be needed in some (e.g., latent population) years.

e. Insecticides. Granular insecticides that are applied to the soil at pegging [R2 plant growth stage, as defined by Boote (1982)] are commonly used to reduce abundance of the lesser cornstalk borer. Several researchers have examined the efficacy of organochlorines against the lesser cornstalk borer (Arthur and Arant, 1956; French, 1971). More recent studies have examined several of the organophosphorus insecticides against this insect (All *et al.*, 1979; Gilreath *et al.*, 1989). Many of these studies measured changes in population densities and assumed that differences were caused by effects of the insecticides. However, determination of the efficacy of a soil insecticide *in situ* is difficult because of immigration and emigration of pest populations, predation and disease effects on pest abundance, and the effects of environmental variables on pesticide degradation.

Mack *et al.* (1989) developed a bioassay procedure using laboratory-grown sorghum seedlings and soil collected from peanut fields that eliminated the problems of predation, disease, and immigration/emigration. The effectiveness of chlorpyrifos, which is the most widely used soil insecticide against the lesser cornstalk borer, was recently determined by this method. A bioassay that used artificial diet instead of sorghum seedlings has also been developed (Miller and Mack, 1990). Mack *et al.* (1991b) found that chlorpyrifos and fonofos significantly reduced larval survival, compared with larval survival in soil from untreated plots, 5 to 14 days after application in four field experiments. Chlorpyrifos was also the only insecticide that was effective for >14 days in all four experiments. The length of effectiveness of chlorpyrifos, as indicated by laboratory bioassay, ranged from 19 to 67 days after treatment.

The effectiveness of all granular insecticides registered for use against the

lesser cornstalk borer probably is reduced in the high soil temperature and low soil moisture associated with lesser cornstalk borer population outbreaks. For example, Harris and Turnbull (1977) noted that the effectiveness of chlorpyrifos and terbufos was reduced in air-dry soil, and Harris and Chapman (1980) reported that technical phorate was inactivated in air-dry sand. Getzin (1985) reported that chlorpyrifos residues that weathered under high temperatures disappeared faster than residues which were exposed to lower temperatures. High soil temperatures increased the degradation rate of insecticides such as carbofuran (Ou *et al.*, 1982), aldicarb, and oxymyl (Bromilow *et al.*, 1980).

Rainfall in the summer is spatially and temporally heterogeneous in the southeastern U.S. which causes a gradation of environmental conditions and hence a range of population densities of the lesser cornstalk borer. It is difficult to determine when to apply an insecticide because of this spatial heterogeneity along with the difficulty in sampling soil insects. Current grower practice in the U.S. is to use a single application of a granular insecticide at the highest labeled rate, so no additional applications would be legally possible. This single application must be timed so that an adequate amount of toxicant is available when outbreak densities of larvae are present.

A good insecticide for the lesser cornstalk borer in peanut should provide consistent control, kill few beneficial arthropods, and be relatively unaffected by the hot, dry conditions that are conducive to population outbreaks of this insect. Plants will be unprotected if an insecticide is applied so early that it degrades and will be unprotected if an insecticide is applied too late. Insecticides that are applied haphazardly may also enhance outbreaks of other insects (Funderburk *et al.*, 1990) or depress the abundance of certain beneficial arthropods (Mack, 1992). Peanut plants are equally susceptible to attack from lesser cornstalk borers from the V9 to the R7 plant growth stages, which lasts for 60 to 70 days (Mack *et al.*, 1988b). None of the currently registered insecticides consistently last for 60 days, and most are inconsistent in their short-term control. Recommended granular insecticides should be applied when most larvae are small to medium-sized and before significant damage to pegs, pods, and the root crown has occurred. Insecticides applied after this damage has occurred may kill larvae, but economic damage will have already occurred. Larvae are difficult to kill when they are in the pods because they are not in direct soil contact, and most granular insecticides need moisture to be moved to that depth.

New insecticide chemistry needs to be developed for management of the lesser cornstalk borer. This insect is exposed to primarily chlorpyrifos in peanut, soybean, and sorghum fields. Resistance to insecticides may occur in this scenario, so we must prepare for future management now.

f. Host plant resistance. Resistance to both plant and pod damage by the lesser cornstalk borer has been reported. Schuster *et al.* (1975) reported that the cultivars Florunner, Florigiant, and Early Runner possess a moderate level of antibiosis to the lesser and were less susceptible than spanish cultivars. Female moths that emerged from the spanish cultivar Spanhoma were more fecund than females emerging from Florunner (Berberet *et al.*,

1982). Greenhouse evaluation of 490 peanut lines in the seedling stage against the lesser cornstalk borer showed a moderate level of resistance to plant damage in Early Runner, Virginia Bunch 67, Florunner, Florigiant, and Dixie Spanish (Smith *et al.*, 1980). Stalker *et al.* (1984) reported that PIs 296116, 262000, 269006, 261955, and 269005 had significantly less damage to pegs and pods by the lesser cornstalk borer than Florigiant. These authors also reported high levels of resistance to the lesser cornstalk borer in several of the wild species of *Arachis*.

Southern Corn Rootworm. The southern corn rootworm, *D. undecimpunctata howardi*, is a major pest of peanut in the Virginia-Carolina growing area (Campbell and Wynne, 1985) and on heavier, poorly drained soils in the southeastern U.S. (Womack *et al.*, 1981). Overwintering adults prefer to oviposit in moist, dark soil with moderate levels of organic matter and clay (Brust and House, 1990b). Most eggs are laid within 3 cm of a host stem. The presence of weeds increases oviposition and influences ovipositional preference with regard to soil texture and moisture (Brust, 1990). Low soil moisture, clay content, and organic matter reduce survival of eggs and first instars (Brust and House, 1990a). Survival, especially for the mobile larval stages, also is low in sand where abrasion of the cuticle by silica particles may increase mortality (Brust and House, 1990a). Adults can feed on peanut leaves, but prefer to feed and oviposit in areas with broadleaf weeds (Brust and House, 1990b).

Rootworm larvae occasionally feed on roots of peanut, but their greatest damage is produced by their feeding on developing pegs and pods. Larvae feed on young pods prior to the hardening of the mesocarp (Fink, 1916) and tunnel into the developing pod. They make an almost cylindrical entry hole in the pod where the larvae feed on immature pod and seed tissue. In addition to direct plant injury caused by larval feeding, damage to pods enhances invasion and establishment of microorganisms. Three to four generations of rootworms occur each year in the southern U.S., while only one generation occurs at the more northern latitudes (Hays and Morgan, 1965).

a. Biological control. Until recently, the natural enemy complex attacking the southern corn rootworm had received little attention. Smith and Barfield (1982) list three species of tachinid parasites, parasitic nematodes, and fungi as natural enemies of *Diabrotica* spp. Brust and House (1988) and Brust (1990, 1991) listed 17 species of natural enemies of the southern corn rootworm, which included carabid larvae and adults, cantharid larvae, staphylinid adults, ants (*Lasius* spp. and *Pheidole* spp.), Diplura larvae (Diplura: Japygidae), and Gamasina and acarid mites (Acaridae: Acarinae). Only ants preyed on all stages of rootworms. Seven species of predators attacked immature rootworms and reduced populations, with the greatest mortality in eggs and first instars. The most successful egg predators are Gamasina mites, *Tyrophagus putrascentia* Schrank (an acarid mite), and ants. Carabid and cantharid larvae, and Gamasina mites are the most important predators of first-instar rootworms, while cantharids, carabids, and ants are most important as predators of second and third instars.

Significantly more acarid and mesostigmatid mites are found in no-tilled than in conventionally tilled peanut. Abiotic factors such as soil moisture have the greatest influence on rootworm survival in conventionally tilled peanut, while biotic factors determined survival in no-tilled peanut.

Brust and House (1990b) also reported that predators and weeds in peanut indirectly reduced pod damage by rootworms; peanut in weedy areas have more predators and fewer damaged pods than peanut in nonweedy areas. As noted above, adult *Diabrotica* feed and oviposit in weedy areas. Brust and House (1990b) suggested that the structural complexity of weed roots interact positively with the predator complex to reduce southern corn rootworm damage in peanut.

In addition, a new strain of *B. thuringiensis*, EG4961, has recently been discovered that produces a crystalline protein during sporulation that is toxic to both adults and larvae of several Coleoptera, including the southern corn rootworm (Johnson *et al.*, 1993). This unique strain of *B. thuringiensis* offers potential for microbial control of this important soil-inhabiting pest of peanut.

b. Host plant resistance. Resistance to *D. undecimpunctata howardi* has been reported in several peanut cultivars (see Lynch, 1990 for a review). Among the most important genotypes are GP-NC 343 and NC 6 (Campbell *et al.*, 1971, 1977; Campbell and Wynne, 1980, 1985). As noted by Smith and Barfield (1982), the parents of NC 6, GP-NC 343 and VA 61R, are both susceptible to rootworm injury in greenhouse evaluations, suggesting that resistance is related to multiple factors acting in the field but not in the greenhouse. The cultivar NC 6 is adapted to heavier soils of the Virginia-Carolina area where the use of cultivars with resistance to rootworms is one of the major management strategies. Campbell and Wynne (1985) showed that insecticide rates could be reduced by 60 to 80% when planting NC 6 and still obtain insect control comparable with the recommended insecticide rate when planting Florigiant.

c. Pheromone traps. Brandenburg *et al.* (1992) evaluated pheromone traps for monitoring populations of adult male rootworms in peanut fields. Pod damage by rootworms was not consistently related to numbers of males captured in the pheromone traps. However, fields in which $\leq$45 beetles/trap/week were captured had <3% damaged pods and appeared to be at low risk for southern corn rootworm damage.

INTRACELLULAR FEEDING GUILD OF ARTHROPODS ATTACKING PEANUT

Intracellular Feeders and Plant Injury

Peanut is attacked by a variety of intracellular feeders including aphids, leafhoppers, thrips, whiteflies and mites (Table 4). These insects damage peanut directly by removing photosynthate and indirectly by their transmission of plant diseases. Intracellular feeders either insert their mouthparts into plant cells or rasp the cells and consume the fluids. Disease transmission by

intracellular feeders (Table 6) is especially important because, once a plant is infected, there are no curative measures for alleviating the disease in the plant. Economic losses in peanut from pathogens transmitted by insects often exceed losses caused by the insect injury itself. For example, rosette transmitted by *Aphis craccivora* Koch decimated peanut yield in West Africa in 1975 (Gibbons, 1977). Likewise, bud necrosis in India and tomato spotted wilt in the U.S. are extremely important diseases that are transmitted by thrips (Wightman and Amin, 1988; Todd *et al.*, 1993).

Recent research on the feeding behavior of the potato leafhopper, *Empoasca fabae* (Harris), revealed that it more commonly uses a lacerate and flush feeding technique—i.e., stylet movement through and laceration of several layers of cells with simultaneous secretion of salivary fluids, occasionally followed by ingestion (Kabrick and Backus, 1990)—rather than a stylet-sheath formation method of feeding. The lacerate and flush injury disrupts

Table 6. Intracellular feeding guild of major insect pests of peanut [modified after Lynch *et al.*, 1986; Wightman *et al.*, 1990; Gahukar, 1992; and Lynch and Douce 1992 (for a more comprehensive list of arthropods that feed on peanut, see Smith and Barfield, 1982)].

Group/taxon	Common name	Distribution
Aphids		
Aphis craccivora Koch	Groundnut aphid	Africa, Asia, Americas
Leafhoppers (Jassids)		
Empoasca dolichi Paoli		Africa
Empoasca fabae (Harris)	Potato leafhopper	Americas
Empoasca facialis Jacobi		Africa
Empoasca kerri Pruthi	Groundnut jassid	Asia
Lygaeid		
Elasmolomus sordidus Fabricius	Lygaeid bug	Africa
Thrips		
Caliothrips indicus (Bagnall)	Sesbania thrip	Africa, Asia
Frankliniella fusca (Hinds)	Tobacco thrips	Americas
Frankliniella occidentalis (Pergande)	Western flower thrips	Americas
Frankliniella schultzei (Trybom)	Cotton bud thrips	Africa, Asia
Scirtothrips dorsalis Hood	Chilli thrips	Asia
Thrips palmi Karny[a]	Melon thrips	Asia, U.S.
Whitefly		
Bemisia tabaci (Gennadius)[b]	Sweetpotato whitefly	Africa, Asia, Americas
Acari		
Tetranychus urticae Koch	Twospotted spider mite	Africa, Asia, Americas

[a]Introduced into Florida in 1989.

[b]A new, more virulent strain B was reported on peanut in the U.S. in 1987 and has the potential to become a major pest. Strain B has been described as a new species, *B. argentifolii* Bellows and Perring (Bellows *et al.*, 1994).

vascular bundles, causes hyperplasia of cambial cells into the phloem area, and crushes sieve elements and phloem as the cambial cells expand and enlarge (Kabrick and Backus, 1990). They hypothesized that short-duration probes with simultaneous injection of salivary fluids leave partially damaged, living cells. The insect injects sufficient saliva to initiate a sequence of biochemical reactions that cause hyperplasia of cambial cells that block the phloem and prevent translocation of photosynthates.

Feeding by the twospotted spider mite, *Tetranychus urticae* Koch, produces similar physiological responses in peanut. Plant injury by feeding *T. urticae* is primarily restricted to the spongy mesophyll but may extend to the parenchyma (Hislop and Jeppson, 1976). Leaf injury by mites decreases photosynthesis and transpiration in severely damaged cells; it also increases transpiration in moderately damaged leaves, causes development of smaller or deformed leaves, and lowers leaf chlorophyll content (Atanasov, 1971; Hall and Ferree, 1975). Photosynthesis is reduced in injured leaves from inhibition of gas exchange (DeAngelis *et al.*, 1983b). Leaf transpiration and water loss increase at night in injured leaves and, combined with increased water loss from mite injury of plant tissue, cause water stress during the day and closure of the leaf stomates (DeAngelis *et al.*, 1982). The increase in water stress reduces the fresh weight of leaves and increases soluble carbohydrates in injured leaves (DeAngelis *et al.*, 1983a).

Leafhoppers. Probably the most conspicuous symptom of plant damage to peanut by an intracellular feeder is the "hopperburn" caused by the potato leafhopper. Both adults and nymphs prefer young leaves where their feeding causes yellowing of leaflets. Damage symptoms initially appear as whitening of the veins followed by a "V"-shaped yellowing of the tips of the leaflets; with severe injury, necrosis of the damaged tissue occurs (Womack *et al.*, 1981).

In the U.S., the potato leafhopper is unable to survive the winter in more northern latitudes and overwinters in mild climates along the Gulf Coast. Populations increase in the spring and adults migrate northward on wind currents associated with weather fronts (Taylor, 1985). Dispersing adults may reach Canada in early June where they damage potato, peanut, and other crops (Ellis, 1984). Females lay their eggs in tissue near the leaf midrib and veins or in stems. Nymphs and adults prefer to feed on the underside of young leaves. Amin (1988) noted that feeding by leafhoppers may reduce plant weight by 18% and pod yield by 9%. Ellis (1984) reported that early leafhopper infestations reduce the number of leaves/plant in peanut in southwestern Ontario; over 40 leafhoppers/plant, an extremely high density, are necessary to reduce yield.

Smith *et al.* (1985) developed criteria for estimating potato leafhopper damage to peanut by measuring percentage of damaged leaflets, chlorotic area, necrotic area, and total percent damage relative to total leaflet area. Significant correlation coefficients were noted for percentages of chlorosis with leaflet damage (0.74 to 0.85), necrosis with total damage (0.62 to 0.89), and leaflet damage with total damage (0.76 to 0.92). They concluded that the percentage of leaflets damaged is a good indicator of plant damage by the potato leafhopper.

a. Biological control. Natural enemies of *Empoasca* include lygaeid bugs (Nair, 1986), spiders (Amin, 1988; Agnew and Smith, 1989), a fly (*Crossopalpus* sp.) (Nandagopal, 1988), and several parasitoids [*Chalarus latifrons* Hardy, *Aphelopus* sp., *Anagrus armatus* (Ashmead), *A. nigriventris* Girault, *A. epos* Girault, and *Paracentrobia subflava* (Girault)] (Freytag, 1985).

b. Host plant resistance. A considerable number of peanut accessions have been identified, particularly among the North Carolina accessions, with resistance to *E. fabae* and *E. kerri* Pruthi (for reviews, see Lynch, 1990; Wightman *et al.*, 1990). Resistance is associated with a thick adaxial epidermis, longer trichomes, and a higher percentage of straight trichomes on the underside of leaflets (Campbell *et al.*, 1976). In addition, Amin (1982) noted that resistance is enhanced by larger tannin-filled cells and by phloem tissue surrounded by thick-walled sclerenchyma cells. *Empoasca kerri* is less fecund and has reduced nymphal survival and reduced adult emergence when feeding and ovipositing on NC Ac 2214, a highly resistant line, than on a susceptible line (P. W. Amin, pers. commun., 1990). Genetic analysis of characteristics associated with leafhopper resistance in peanut showed that long trichomes on the adaxial surface of leaves, leaf midrib, and petiole were determined by nonadditive genetic variation, but additive variation is important for long trichomes on the midrib and petioles and reduced leafhopper damage (Dwivedi *et al.*, 1986). In addition, they noted that NC Ac 2230, a highly resistant line with stable resistance, has a high general combining ability for long trichomes, making it an excellent parent in crosses, while maintaining leafhopper resistance.

GP-NC 343, a line with moderate resistance to thrips, termites, and corn earworm, also has moderate resistance to both *E. fabae* and *E. kerri* and is used as the standard for comparison of other lines for leafhopper resistance (Campbell and Wynne, 1980; Amin *et al.*, 1985). NC 6, a commercial virginia-type cultivar, has resistance to the southern corn rootworm, and moderate resistance to thrips, leafhoppers, and the corn earworm (Campbell and Wynne, 1980).

In addition to the above cultivars, wild species of *Arachis* have an extremely high level of resistance to leafhoppers. Resistance to the potato leafhopper has been reported in *A. batizocoi, A. diogoi* (formerly *A. chacoensis*), *A. correntina, A. duranensis, A. glabrata, A. macedoi, A. monticola, A. paraguariensis, A. pusilla, A. rigonii, A. repens, A. stenosperma,* and *A. villosa* (Campbell and Wynne, 1980; Stalker and Campbell, 1983). Hybrids between *A. hypogaea* and compatible wild species also are resistant to several species of insects, including the potato leafhopper, and show potential for introgressing resistance from the wild species into the cultivated species.

Thrips. Eighteen species of thrips are injurious to peanut (Smith and Barfield, 1982; Wightman *et al.*, 1990). *Frankliniella fusca* (Hinds), the tobacco thrips, is the most abundant species on peanut in the U.S. (Mitchell and Smith, 1991; Mulder *et al.*, 1991; Chamberlin *et al.*, 1993), while *Scirtothrips dorsalis* Hood and *Caliothrips indicus* (Bagnall) are most

frequently encountered in Southeast Asia (Amin, 1988; Wightman *et al.*, 1990). Both adult and immature thrips are small, inconspicuous insects most often found in the terminals and flowers of peanut. Eggs are inserted in the tissue of their host. Immature thrips are wingless, while adults may be macropterous or brachypterous, depending on the species and season (Chamberlin *et al.*, 1992). Immature thrips have two actively feeding larval stages followed by two pupal stages. Both adults and larvae pierce plant cells and consume exuding fluids.

Lynch *et al.* (1984) concluded that controlling the tobacco thrips with insecticides usually does not increase yield enough to offset the cost of control. However, two significant findings have altered opinions on the importance of thrips on peanut. First, thrips injury and herbicide injury on seedling plants interact significantly to reduce main stem height, canopy width, yield, and value of peanut (Herbert *et al.*, 1991). Insects, such as thrips, that sap photosynthates reduce the size of the carbohydrate pool available for growing new shoots, roots, leaves, and pods (Fig. 5) (Gutierrez *et al.*, 1975). Most plants maximize leaf area production early in the season to increase photosynthate production and partition the photosynthate to leaves, shoots, and roots for rapid vegetative growth (Ketring *et al.*, 1982). A decline in the flow of nutrients and water during these stages, coupled with other stresses, adversely affects plant growth (Boote *et al.*, 1980). Legumes such as peanut also greatly reduce the flow of photosynthate during the reproductive phase of plant growth, with photosynthate shunted to developing fruit. Removal of photosynthate by insects early in vegetative growth would often be inconsequential, based on a photosynthate pool model. For example, a plant could compensate for early season injury by shunting more carbohydrate to the production of new leaves and less to formation of new roots, if soil moisture was adequate. However, removal of photosynthates early in the growing season would be serious if (a) the plant was stressed by other factors (e.g., drought, herbicide injury, etc.) or (b) a large enough amount of photosynthate was removed to permanently decrease the size of the photosynthate pool and limit plant growth. The combination of early thrips injury coupled with herbicide injury and/or poor growing conditions

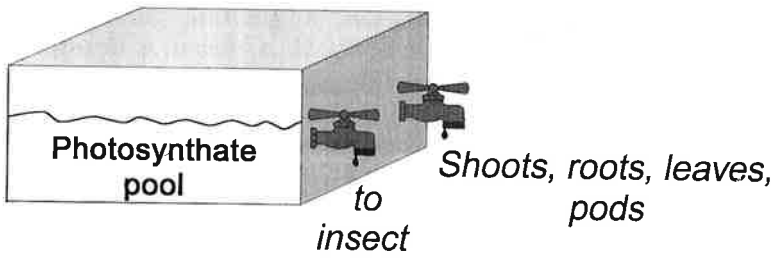

Fig. 5. Conceptual diagram of the removal of photosynthate by insects from the photosynthate pool intended for growth of new shoots, roots, leaves, or pods.

later in the season may interact to permanently reduce the photosynthate pool, limit plant growth, and reduce yield.

a. Thrips as vectors of virus diseases. Secondly, and most importantly, thrips are important pests of peanut as a vector of tomato spotted wilt virus (TSWV) and bud necrosis virus (BNV) to peanut. BNV has long been one of the more important diseases of peanut in Asia (Reddy and Wightman, 1988). Epidemics of TSWV in peanut were first noted in the U.S. in south Texas in 1986 (Stewart *et al.*, 1989). In the southeastern U.S., TSWV was detected in peanut in 1987 and its incidence has increased substantially in the ensuing years (Culbreath *et al.*, 1992). The incidence of TSWV in highly infected fields in Georgia have exceeded 60% in 1993 (A. K. Culbreath and J. W. Todd, pers. commun., 1993).

Thrips also vector several other important viruses to peanut (Table 7). Recently, the tospoviruses (i.e., TSWV, BNV, peanut yellow spot, and impatiens necrotic spot) were divided into distinct groups based on nucleocapsid proteins (German *et al.*, 1992). TSWV, the most important tospovirus of peanut in the U.S., is transmitted by *F. fusca* and *F. occidentalis* (Pergande), while BNV and yellow spot are the most important tospoviruses

Table 7. Major insect vectors and viral diseases of peanut (modified after Porter *et al.*, 1984; Wightman and Amin, 1988).

Group/taxon	Virus vectored	Hosts	Type transmission
Aphids			
Aphis craccivora (Koch)	Rosette	Primarily legumes	Persistent; no seed transmission
	Peanut mottle	Cultivated and wild legumes	Nonpersistent sap transmission; low seed transmission
	Peanut stunt	Primarily legumes	Nonpersistent; low seed transmission
	Peanut stripe	Wide range	Nonpersistent; up to 30% seed transmission
	Eyespot	Unknown	Nonpersistent sap transmission
	Green/mosaic	Wide range	Nonpersistent sap transmission
Thrips			
Frankliniella fusca (Hinds) *F. occidentalis* (Pergande) *F. schultzei* (Trybom)	Tomato spotted wilt	Wide range	Persistent sap inoculation; no seed transmission
F. schultzei (Trybom) *Thrips palmi* Karny	Bud necrosis	S.E. Asia	Persistent sap inoculation; no seed transmission
Scirtothrips dorsalis Hood	Peanut yellow spot	S.E. Asia	Persistent sap inoculation; no seed transmission
Whiteflies			
Bemisia tabaci (Gennadius)	Cowpea mild mottle	Wide range	Nonpersistent sap transmission

vectored to peanut in Southeast Asia (Wightman and Amin, 1988; Todd *et al.*, 1993). BNV is vectored primarily by *F. schlutzei* (Trybom) and *Thrips palmi* Karny, and peanut yellow spot is vectored by *S. dorsalis* (Wightman and Amin, 1988; German *et al.*, 1992; Todd *et al.*, 1993). Thrips acquire tospoviruses as immatures after feeding on an infected plant for *ca.* 30 min. A latent period of *ca.* 10 days after acquisition appears to be required before transmission of the virus by adult thrips (Reddy and Wightman, 1988; German *et al.*, 1992).

Research on BNV and TSWV was recently reviewed by Reddy and Wightman (1988). The incidence of BNV in peanut in India is correlated with density of the principle vector, *F. schultzei*. Favorable climatic conditions for thrips population increases and migration (i.e., a temperature from 20 to 30 C combined with little rainfall) enhance spread of BNV. Plant populations also play an important role in determining the incidence of BNV in peanut. The number of plants infected with BNV remains constant as plant populations increase. Therefore, the percentage of infected plants declines as plant populations increase. Amin and Mohammad (1980) concluded that primary immigration of thrips infected with BNV was most important to dispersal of the virus and that secondary spread is not important to its dispersal. Infection with BNV during vegetative growth of peanut causes severe stunting of the infected plant with little or no pod production. Infection during flowering and pegging reduces yield by decreasing the number of flowers, the duration of the flowering period, pod length, and pod growth. Later infection with BNV affects plant processes and yield to a lesser extent (Amin and Mohammad, 1980).

BNV in peanut may be managed by employing cultural practices that limit the activity of thrips during critical plant growth stages or by genetic resistance to the vector, the virus, or both (Reddy and Wightman, 1988). Cultural methods for controlling BNV in peanut include (a) applying good agronomic practices (i.e., planting seed with high germination, optimal seed spacing, fungicides on seeds, etc.) that result in rapid germination and growth of plants; (b) planting peanut when populations of important viral vectors are low; (c) planting a high plant density; and (d) intercropping peanut with fast growing, tall cereals that restrict movement of thrips (Reddy and Wightman, 1988).

Life-fertility tables reveal that *F. fusca* survive and reproduce better on peanut than *F. occidentalis* (Lowry *et al.*, 1992). Female *F. occidentalis* live for only 2 days on peanut leaflets and survival of the immatures is <20% at 20-25 C, and immatures fail to survive at 30 C. Conversely, the capacity for *F. fusca* populations to increase is greatest at 30 C. Puche and Funderburk (1992) also concluded that peanut was an excellent host for *F. fusca*. Because of its ability to survive and reproduce on peanut, Lowry *et al.* (1992) concluded that *F. fusca* is probably the most important vector for secondary spread of TSWV in the U.S.

Research on vector ecology and epidemiology of TSWV in Georgia was recently reviewed by Todd *et al.* (1993). During winter and early spring, *F. occidentalis* was collected in Georgia from 44 species of plants, and *F. fusca*

was collected from 25 species (Chamberlin *et al.*, 1992). *Frankliniella occidentalis* was most abundant on *Trifolium* spp. in the spring, while *F. fusca* was most abundant on volunteer peanut. Thrips adults collected in the late fall or early spring from volunteer peanut were primarily brachypterous *F. fusca*. TSWV was detected in both brachypterous *F. fusca* adults and volunteer peanut in both the fall and spring, suggesting that the virus may overwinter on volunteer peanut and/or in brachypterous thrips in harvested peanut fields in Georgia (Chamberlin *et al.*, 1993). Barbour and Brandenburg (1994) reported that in-field emergence of thrips in locations previously planted to peanut was not an important source of the insect. In Georgia, however, an extremely low percentage of the adult thrips colonizing peanut in the early spring was viruliferous (Todd *et al.*, 1993). Application of systemic insecticides to control thrips in peanut did not prevent infection with TSWV (Todd *et al.*, 1992). The incidence of TSWV was consistently higher in peanut when aldicarb or acephate were applied in-furrow at planting than in untreated peanut; application of phorate at planting resulted in an infection rate equal or greater than in untreated peanut. Application of acephate weekly throughout the growing season provided excellent control of thrips larvae but reduced the incidence of TSWV by only *ca.* 50% compared with an untreated control. Acephate killed the larvae which should have limited the acquisition of the virus from an infected, insecticide-treated plant, limited movement of larvae from plant to plant to spread the virus, and limited secondary transmission. Thus, the increase in virus incidence in the treated fields was due to primary infection as adult thrips continuously/sporadically migrated into peanut fields throughout the growing season (Todd *et al.*, 1993).

Research in Texas on the incidence of TSWV in peanut planted on different dates has revealed a "window" in which planting may result in a lower incidence of infection (F. L. Mitchell and J. W. Smith, pers. commun., 1993). The window was detected by recording the planting date for each field and routinely recording the number of TSWV-infected plants over a period of 3 years. Each field was divided into quadrants and a 30.5-m transect was established in each quadrant. The number of infected plants along the transect was recorded weekly. A plot of incidence of virus infection by planting date showed that peanut planted before May 7 or after mid-June had a higher incidence of TSWV than peanut planted within the window. The window may be due to a reduced abundance and/or activity of thrips at certain times of the growing season as was suggested for cultural management of the BNV by Reddy and Wightman (1988).

b. Biological control. The most comprehensive treatise on the natural enemies of thrips is that of Lewis (1973). Thrips are attacked by several generalists predators and parasites. Predators include a predatory thrips, *Franklinothrips* sp. (Ananthakrishnan, 1973); anthocoreid bugs, *Orius maxidentex* Ghauri and *O. tantillus* (Motsch.); and the bug *Carayonocoris* sp. (Muraleedharan and Ananthakrishnan, 1978). In addition, Lewis (1973) lists a big-eyed bug (*Geocoris* sp.), lacewings (*Crysopa* sp. and *Hemerobius* sp.), a coccinellid (*Cheilomenes vicina* Mulsant), a syrphid (*Ishiodon aegypticus*

Weid), and a mirid (*Psallus* sp.) as predators of thrips. Members of the Trichomattidae, Scelionidae, and Mymaridae parasitize thrips eggs and Eulophidae parasitize immature thrips (Lewis, 1973).

c. Host plant resistance. Several sources of resistance in peanut to *F. schultzei* have been identified at ICRISAT in India (for review, see Lynch, 1990). The cultivar Robut 33-1 is resistant to thrips and shows a reduced incidence of infection by BNV in the field (Wightman *et al.*, 1990). This cultivar has been used as a parent for ICGS 11 and ICGS 44, high-yielding lines that show resistance to BNV (Nigam *et al.*, 1991). Breeding lines ICGV 86029 and ICGS 86031 are resistant to virus infection (Reddy and Wightman, 1988) and have a low incidence of infection (Nigam *et al.*, 1991). In addition, resistance approaching immunity to BNV has been identified in *A. diogoi* (formerly *A. chacoensis*) (Reddy and Wightman, 1988).

Southern Runner (Culbreath *et al.*, 1992) and Georgia Browne (A. K. Culbreath, J. W. Todd, and W. D. Branch, pers. commun., 1993) have a lower incidence of TSWV infection in the field than Florunner. The incidence of virus infection in Florunner and Southern Runner increases linearly over time, but the increase was more rapid in Florunner than in Southern Runner (Culbreath *et al.*, 1992). Populations of adult and immature thrips are similar on these two cultivars, suggesting that the resistance in Southern Runner may be due to resistance to the virus rather than to resistance to its vector.

Resistance to thrips is also found in the wild species of *Arachis* (Table 8). Yang *et al.* (1993) reported compositional differences in the cuticular lipids from peanut blooms and foliage among the wild species that may be related to their resistance to thrips, fall armyworm, and other insects. Demski *et al.* (1991) reported field resistance to TSWV among the wild species and among plant introductions of *A. hypogaea*. Those entries with no infection 100 days after planting included *Arachis* species PIs 262286, 262828, 276233, 468142, 475883, and S-862; *A. glabrata* PIs 262794 and 338264; and *A. hypogaea* PIs 196621, 339967, and 341267.

Twospotted Spider Mite. The twospotted spider mite, *T. urticae*, is a major pest of peanut in the U.S., particularly in the Virginia-Carolina peanut-producing area (Smith and Mozingo, 1983). The ecology of spider mites was reviewed by Brandenburg and Kennedy (1987), a synopsis of which is presented here. *Tetranychus urticae* overwinters as diapausing females or, in areas with moderate winter temperatures, actively reproducing adults. Diapausing adults pass the winter in sheltered habitats of weedy borders around fields (Margolies and Kennedy, 1985; Brandenburg and Kennedy, 1987). They emerge in the spring, initially feed on early spring hosts, and then become established on corn. *Tetranychus urticae* populations increase rapidly in corn during the tasseling-silking stage (Margolies and Kennedy, 1984). With the cessation of corn growth, mites move upward on the corn plant. Mites orient away from light on windy days, assume a dispersal position by raising their forelegs and forebodies, and disperse to other crops (Smitley and Kennedy, 1988). This dispersal behavior of spider mites continues until corn senesces. The dispersal of mites from senescing corn coincides with peanut flowering and pod development, stages favorable for

Table 8. Sources of resistance to *Aphis craccivora* (*A. cra.*), *Frankliniella fusca* (*F. fus.*), *Tetranychus urticae* (*T. urt.*), *Empoasca fabae* (*E. fab.*), *Aproaerema modicella* (*A. mod.*), *Helicoverpa zea* (*H. zea*), *Spodoptera frugiperda* (*S. fru.*), *S. litura* (*S. lit.*), *Elasmopalpus lignosellus* (*E. lig.*), and *Sphenoptera indica* (*S. ind.*) in wild species of *Arachis*[a].

Section/species	Coll. no./ID	PI no.	Plant no.	*A. cra.*[b]	*F. fus.*[c]	*T. urt.*[d]	*E. fab.*[c]	*H. zea*[c]	*S. fru.*[e]	*S. lit.*[b]	*A. mod.*[b]	*E. lig.*[c]	*S. ind.*[b]
Arachis													
A. batizocoi	9484	298639	-	-	R	-	R	R	-	-	-	-	-
	30079	468325	-	HR	-	-	-	-	-	-	-	-	-
	30081	468327	-	HR	-	-	-	-	-	-	-	-	-
A. cardenasii	10017	262141	-	HR	-	-	-	-	R	-	-	-	-
	36019	475998	1	-	-	-	-	-	-	-	-	-	R
	36033	476012	Y[f]	HR	-	-	-	-	-	-	-	-	R
	36034	476013	YF[f]	HR	-	-	-	-	-	S	-	-	R
	36034	476013	Y0-1[f]	HR	-	-	-	-	-	-	R	-	S
A. correntina	-	-	-	R	-	-	R	R	-	-	-	-	-
	-	261870	-	-	-	-	-	-	R	-	-	-	-
	9530	262808	-	-	R	-	R	R	-	-	S	-	R
	9548	331194	-	-	-	R	-	-	-	-	-	-	-
A. diogoi (formerly *A. chacoensis*)	10602	276235	5	R	R	-	R	R	R	HR	R	-	-
A. duranensis	7988	219823	-	HR	R	-	R	R	-	-	S	-	S
	30065	468201	-	-	-	-	-	-	-	-	R	-	-
	30070	475845	-	HR	-	-	-	-	-	-	-	-	-
	30074	468320	-	-	-	-	-	-	-	-	R	-	-
A. hoehnei	30006	468150	-	R	-	-	-	-	-	-	-	-	-
A. kempff-mercadoi	30085	468331	-	-	-	-	-	-	-	HR	R	-	HR
	35001	475873	-	HR	-	-	-	-	-	-	-	-	-

Table 8 (Continued)

Section/species	Coll. no./ID	PI no.	Plant no.	*A. cra.*[b]	*F. fus.*[c]	*T. urt.*[d]	*E. fab.*[c]	*H. zea*[c]	*S. fru.*[e]	*S. lit.*[b]	*A. mod.*[b]	*E. lig.*[c]	*S. ind.*[b]
A. kuhlmannii	30008	468152	-	R	-	-	-	-	-	-	R	-	-
	30017	468159	-	HR	-	-	-	-	-	-	R	-	-
	30035	468168	-	HR	-	-	-	-	-	-	S	-	HR
A. monticola	-	219824	-	-	R	-	R	-	-	-	-	-	-
	7264	263393	-	-	-	-	-	-	-	R	-	-	-
	30063	468199	-	-	-	-	-	-	-	-	R	-	-
A. stenosperma	408	338279	-	HR	R	-	R	R	-	S	HR	-	S
	409	337308	-	-	-	-	-	-	-	-	HR	-	R
	410	338280	-	HR	R	-	R	R	-	-	HR	-	S
A. valida	30011	468154	-	-	-	-	-	-	-	-	S	-	R
A. villosa	-	261872	-	-	-	-	-	-	R	-	-	-	-
	-	298636	-	-	-	-	-	-	-	-	-	R	-
	-	331196	-	-	R	R	R	-	-	-	-	-	-
	villosa	-	-	R	-	-	-	-	-	HR	-	-	-
A. villosa- correntina	Manfredi #5	-	-	-	R	-	R	R	-	HR	-	-	-
	Manfredi #36	-	-	-	R	-	R	R	-	-	-	-	-
Caulorrhizae													
A. repens	10538	276199	-	-	R	-	R	R	-	-	-	-	-
Erectoides													
A. hermannii	9841	262278	-	-	R	-	-	R	-	-	-	R	-
A. major	10573	276225	-	-	R	-	-	R	-	-	-	-	-
	10576	276228	-	-	R	-	-	R	-	-	-	-	-

Table 8 (Continued)

Section/species	Coll. no./ID	PI no.	Plant no.	*A. cra.*[b]	*F. fus.*[c]	*T. urt.*[d]	*E. fab.*[c]	*H. zea*[c]	*S. fru.*[e]	*S. lit.*[b]	*A. mod.*[b]	*E. lig.*[e]	*S. ind.*[b]
A. major	14444	338320	-	-	R	-	-	-	-	-	-	-	-
	30144	468183	18	-	-	-	-	-	-	HR	-	-	-
A. paraguariensis	565	338297	-	-	-	-	-	-	-	-	-	R	-
	565-6	-	-	-	-	-	-	-	-	-	S	-	HR
	11462	331188	-	-	-	-	-	-	-	-	-	-	R
	11488	331187	-	-	R	-	R	R	-	-	-	R	R
	30109	468357	-	-	-	-	-	-	-	HR	R	-	-
	30124	468370	-	-	-	-	-	-	-	HR	-	-	-
	30134	468176	-	-	-	-	-	-	-	HR	-	-	HR
A. stenophylla	30126	468170	-	HR	-	-	-	-	-	HR	HR	-	-
Extranervosae													
A. macedoi	10127	276203	-	-	R	R	R	R	-	-	-	R	-
A. marginata	*marginata*	-	-	R	-	-	-	-	-	-	-	-	-
A. villosulicarpa	-	263396	-	-	R	-	-	-	-	-	-	-	-
	-	378181	-	-	-	-	-	-	R	-	-	-	-
	villosulicarpa	-	-	-	-	-	-	-	-	-	HR	-	S
Heteranthae													
A. dardani	12943	338452	-	-	R	-	-	R	-	-	-	-	-
Procumbentes													
A. appressipila	9990	261877	-	HR	-	-	-	-	-	-	R	R	R
	9993	261878	-	HR	-	-	-	-	-	-	R	-	HR
	10002	262140	-	HR	R	-	-	R	-	HR	R	-	HR
	30003	468149	-	HR	-	-	-	-	-	-	R	-	HR
	30009	468153	-	HR	-	-	-	-	-	-	R	-	HR

Table 8 (Continued)

Section/species	Coll. no./ID	PI no.	Plant no.	*A. cra.*[b]	*F. fus.*[c]	*T. urt.*[d]	*E. fab.*[c]	*H. zea*[c]	*S. fru.*[e]	*S. lit.*[b]	*A. mod.*[b]	*E. lig.*[c]	*S. ind.*[b]
A. chiquitana	36025	476004	1	-	-	-	-	-	-	-	R	-	HR
A. lignosa	327	338315	-	-	-	-	-	-	R	-	-	-	-
A. kretschmeri	30007	468151	-	R	-	-	-	-	-	R	HR	-	-
A. rigonii	10034	262142	-	-	R	-	R	R	-	-	-	-	-
A. vallsii	30012	-	339	-	-	-	-	-	-	HR	-	-	-
Prorhizomatosae													
A. burkartii	7864	261851	-	-	-	-	-	-	R	-	-	-	-
Rhizomatosae													
A. glabrata	189	-	-	-	-	-	-	-	-	HR	-	-	-
	277	162801	-	-	-	-	-	-	R	-	-	-	-
	335	338317	-	-	-	R	-	-	-	-	-	-	-
	349	338305	-	-	R	-	-	R	-	-	-	-	-
	486	338267	-	-	R	-	R	R	-	-	-	-	-
	571	338265	91B	-	R	-	-	R	-	HR	-	-	-
	1960	-	100	-	R	-	-	R	-	-	-	-	-
	9553	262801	90	-	-	-	-	-	-	HR	-	-	-
	9572	262819	311	-	-	-	-	-	-	HR	-	-	-
	9592	262828	-	-	R	-	-	R	-	-	-	-	-
	9629	262834	315	-	-	-	-	-	-	HR	-	-	-
	9645	262841	-	-	-	-	-	R	-	-	-	-	-
	9649	262844	-	-	-	-	-	R	-	-	-	-	-
	9667	262848	316	-	-	-	-	-	-	HR	-	-	-
	9667	262848	-	-	R	-	-	R	-	-	-	-	-
	9797	262807	-	-	-	-	-	-	-	HR	-	-	-

Table 8 (Continued)

Section/species	Coll. no./ID	PI no.	Plant no.	*A. cra.*[b]	*F. fus.*[c]	*T. urt.*[d]	*E. fab.*[c]	*H. zea*[c]	*S. fru.*[e]	*S. lit.*[b]	*A. mod.*[b]	*E. lig.*[c]	*S. ind.*[b]
A. glabrata	9813	262793	-	-	R	-	-	R	-	-	-	-	-
	9815	262794	-	-	R	-	-	R	-	-	-	-	-
	9830	262797	-	-	R	R	R	R	-	-	-	-	-
	9834	262798	-	-	R	-	-	R	-	-	-	-	-
	9882	262286	-	-	R	-	-	R	-	-	-	-	-
	9893	262287	-	-	R	-	-	R	-	-	-	-	-
	9893	262287	321	-	-	-	-	-	-	HR	-	-	-
	9921	262296	100	-	-	-	-	-	-	HR	-	-	-
	9966	262306	-	-	R	-	-	R	-	-	-	-	-
	10596	276233	-	R	R	R	-	R	-	-	-	-	-
	10596	276233	C	-	-	-	-	R	-	-	-	-	-
	30114	468361	-	-	-	-	-	-	-	HR	-	-	-
	30116	468363	19	-	-	-	-	-	-	HR	-	-	-
	30120	468367	13	-	-	-	-	-	-	HR	-	-	-
	30122	468369	-	-	-	-	-	-	-	HR	-	-	-
	30132	468175	1	-	-	-	-	-	-	HR	-	-	-
	30135	468177	21	-	-	-	-	-	-	HR	-	-	-
	30138	468179	3	-	-	-	-	-	-	HR	-	-	-
	Florigraze	-	-	-	-	-	-	-	R	-	-	-	-
A. glabrata var. *hagenbeckii*	A45/115	-	-	-	-	-	-	-	-	HR	-	-	-
	A27/117	-	-	-	-	-	-	-	-	HR	-	-	-
	2A5	-	-	-	-	-	-	-	-	HR	-	-	-
A. pseudovillosa	9634	262836	-	-	-	-	-	-	-	R	-	-	-
	10566	276223	-	-	R	R	-	R	-	-	-	-	-

Table 8 (Continued)

Section/species	Coll. no./ID	PI no.	Plant no.	*A. cra.*[b]	*F. fus.*[c]	*T. urt.*[d]	*E. fab.*[c]	*H. zea*[c]	*S. fru.*[e]	*S. lit.*[b]	*A. mod.*[b]	*E. lig.*[c]	*S. ind.*[b]
Triseminatae													
A. triseminata	12922	338449	-	HR	R	-	R	R	-	-	R	-	HR
Unknown													
Arachis sp.	-	338454	-	-	R	-	-	R	-	-	-	-	-
	A77/113	-	-	-	-	-	-	-	-	HR	-	-	-

[a]S = susceptible; R = resistant; HR = highly resistant. The assistance of T. Stalker and R. Pittman in preparing this table is gratefully acknowledged.

[b]Germplasm evaluated at the International Crops Research Institute for the Semi-Arid Tropics, Hyderabad, India (J. A. Wightman, G. V. Ranga Rao, and J. P. Moss, pers. commun., 1993) or reported by Amin and Mohammad (1980) and Amin (1985).

[c]See Lynch (1990) for references.

[d]Johnson *et al.* (1977).

[e]Lynch *et al.* (1981).

[f]Y and YF = yellow-flowered plants; YO = yellow and orange-flowered plants.

mite colonization and rapid population increase (Margolies and Kennedy, 1984). When peanut matures, mites disperse to field borders where they either feed on winter hosts or hibernate to complete the cycle. Thus, in the Virginia-North Carolina peanut growing areas, twospotted spider mite populations in corn are indicative of potential spider mite problems in peanut.

Mite outbreaks in peanut are thought to be caused by an interaction between fungicides and insecticides which reduced populations of natural enemies, both fungal pathogens and arthropod predators (Campbell, 1978). The use of fungicides enhanced mite population increases more than the use of insecticides, but tank mixes of insecticides and fungicides, or their application on alternate weeks, resulted in mite outbreaks (Campbell, 1978). Brandenburg and Kennedy (1983) showed that the fungicide benomyl inhibited conidial germination and growth of *Neozygites floridana* (Weiser and Muma), an important fungal pathogen of spider mites in peanut. However, no evidence was found that pesticides reduced the number of predators in peanut or that predators play a major role in the regulation of mite populations in peanut (Boykin *et al.*, 1984a). Boykin and Campbell (1982) showed that mites reared on peanut leaves treated with mancozeb, carbaryl, and mancozeb plus carbaryl have slightly elevated intrinsic rates of increase than mites reared on untreated foliage. Boykin and Campbell (1984) also found that the application of several fungicides, insecticides, or combinations of these on peanut results in population increases and dispersal of mites.

Cultural practices also influence *T. urticae* in peanut. Boykin *et al.* (1984b) reported that the number of mites moving into peanut is inversely related to the width of barren soil borders around peanut fields. Control of vegetation around field margins also impacts spider mites. Application of paraquat to kill vegetation along field borders had no influence on the number of mites entering the peanut field, but mowing weedy borders surrounding a peanut field increased mite infestations in the field.

Microclimate temperature may play a critical role in the development of twospotted spider mite outbreaks in peanut, as it does in other crops. For example, peppermint (*Mentha piperita* L.) and strawberry [*Fragaria chilosensis* (L.) Duch. x *virginiana* Duch.] leaves infested with twospotted spider mites have abnormal closure of stomates (DeAngelis *et al.*, 1982). Stomate closure in hot, dry weather increased daily canopy temperatures by 4 C (Toole *et al.*, 1984). The increase in temperature as stomates close would decrease generation time of spider mite populations leading to an outbreak of mites. Irrigation reduces canopy temperature and may be an effective method of reducing the probability of mite outbreaks.

a. Biological control. The fungus *N. floridana* is probably the major regulator of spider mite populations. This fungus infects a high percentage of mites during sustained periods of high relative humidity or free moisture (Brandenburg and Kennedy, 1987). Under appropriate environmental conditions, *N. floridana* decimates mite populations prior to its aerial dispersal from corn, in which case damaging infestations did not develop in peanut

(Brandenburg and Kennedy, 1987).

Several species of predators feed on spider mites in peanut (Boykin *et al.*, 1984a; Agnew and Smith, 1989). These include spiders, predaceous thrips, predaceous mites, *Orius insidiosus* (Say), *Hippodamia convergens* Guérin-Méneville, and *Scymnus* spp.

b. Host plant resistance. Lynch (1990) lists several sources of resistance in peanut to *T. urticae* and *T. tumidellus* Prichard and Baker. Moderate levels of resistance to the twospotted spider mites have been reported in GP-NC 343, NC Ac 302, NC Ac 469, NC Ac 827, NC Ac 17347, NC Ac 17367, and GK-53 (Johnson *et al.*, 1980, 1982). Analysis of nutrients in peanut leaves showed that mite damage is negatively associated ($r^2 = -0.69$) with carbohydrate and calcium of leaves (Johnson and Campbell, 1982). Much higher levels of resistance to spider mites have been reported among the wild species of *Arachis*. Leuck and Hammons (1968) found resistance to *T. tumidellus* in *Arachis* sp. (PI 268241), *A. villosulicarpa* (PI 263396), and *A. repens*. Johnson *et al.* (1977, 1980) reported resistance to *T. urticae* in the sections *Rhizomatosae* (PIs 262286, 262827, 262840, 338296, and 338317), *Arachis* (PI 331194), *Extranervosae* (PI 276203), and *Erectoides* (PI 262142). Selections from the *Rhizomatosae* were essentially free of mites throughout a 5-month test period. Egg production was greatly reduced when mites fed on PIs 262286 and 262840 due to a high level of nonpreference that mites exhibited on these lines. Tolerance, nonpreference and antibiosis mechanisms of peanut resistance to *T. urticae* were identified (Johnson *et al.*, 1977, 1980, 1982).

Aphids. *Aphis craccivora*, the groundnut aphid, is an important vector of viral diseases in peanut (Table 7). Smith and Barfield (1982) and Wightman *et al.* (1990) give excellent reviews of the biology/ecology and natural enemies of *A. craccivora*. Rosette is probably the most important virus transmitted by *A. craccivora* and remains a major constraint to peanut production in Africa today. Rosette is caused by two viruses, rosette assistor virus and rosette satellite virus; both must be transmitted to peanut by aphids for maximum expression of symptoms (Reddy and McDonald, 1991).

a. Biological control. Several coccinellids—*Menochilus sexmaculatus* (Fab.), *Coccinella septempunctata* Fab., and *Brumoides suturalis* Fab.; a chrysopid, *Chrysopa carnea* Steph.; and syrphid larvae, *Paragus* spp. and *Syrphus* spp.—are important predators of the groundnut aphid (Khan and Hussain, 1965). The braconid *Aphidius colemani* and the encyrtid *Psyllaephagus pulvinatus* are important parasites of *A. craccivora* in Malawi (Farrell, 1976). In addition, entomophagous fungi are important pathogens of the groundnut aphid during the latter part of the growing season.

b. Host plant resistance. Several sources of resistance in peanut have been reported to *A. craccivora* and/or rosette (for review, see Lynch, 1990). Aphids feeding on GP-NC 343, ICGV 86030, and EC 36892 (ICG 5240) exhibit slower nymphal growth and a reduced fecundity than aphids on more susceptible lines (Padgham *et al.*, 1990). EC 36892 has the most consistent detrimental impact on *A. craccivora*; fewer nymphs are produced and nymphal development is slower on EC 36892 than on the susceptible TMV

2. Aphid populations also develop slower and decline faster on EC 36892 than on TMV 2. No initial differences are noted in number of alates that alight on EC 36892 versus TMV 2, but after approximately 10 hr, more aphids are found on TMV 2. Chemical analysis identified an isoflavonoid that slightly inhibits initial probing by *A. craccivora* and a high concentration of procyanidin, a condensed tannin, in the phloem sap that inhibits prolonged ingestion (Padgham *et al.*, 1990). Grayer *et al.* (1992) reported a negative relationship between concentrations of procyanidin in leaf terminals and fecundity of *A. craccivora*. Aphids feeding on EC 36892, the genotype with the highest concentration of procyanidin, produced significantly fewer offspring than aphids on genotypes with lower levels of procyanidin. Wightman *et al.* (1990) noted that *A. craccivora* responded differently in Asia to the antibiosis found in EC 36892 than the aphid in Africa, which may indicate the existence of aphid biotypes.

Other sources of peanut resistance to the groundnut aphid include NC Ac 2214(7) and NC Ac 2214(8) (Amin and Mohammad, 1980), GBPRS-15, AH-7983, Faizpur 1-5, and AH-8048 (Wightman *et al.*, 1990; Gahukar, 1992). Several wild species of *Arachis* also have been identified with resistance to the groundnut aphid. In particular, female *A. craccivora* caged on *A. villosa, A. glabrata, A. diogoi* (formerly *A. chacoensis*), and *A. duranensis* produced 0, 0, 2, and 43 nymphs, respectively, whereas females caged on the susceptible TMV 2 produced over 1000 nymphs (Amin, 1985). Similarly, a high level of resistance to the rosette virus has been identified in cultivars RMP 12 and RMP 91 (Bockelee-Morvan, 1983), and in *A. repens* and *A. glabrata* (Gibbons, 1969).

Sweetpotato Whitefly. The sweetpotato whitefly, *Bemisia tabaci* (Gennadius), was first reported as a pest of peanut in India (Pruthi and Samuel, 1942). In the U.S., the sweetpotato whitefly was reported as a pest of peanut in Florida in 1987 (F. A. Johnson, pers. commun., 1992) and was subsequently reported on peanut in Georgia and Texas. Its infestations on peanut coincided with the identification of a new strain of the sweetpotato whitefly, strain B or poinsettia strain (as opposed to the original sweetpotato whitefly, strain A or cotton strain) that devastated vegetable production in Florida, California, Arizona and Texas (Byrne *et al.*, 1990; Perring *et al.*, 1992). Lynch and Simmons (1993) verified that strain B was indeed the whitefly found on peanut in Georgia. However, Bellows *et al.* (1994) suggested that the two strains may represent two distinct species of whiteflies. This hypothesis was supported by research that showed an absence of interspecific copulation, and differences in allozyme frequencies and single-primer PCR-amplified DNA sequences (Perring *et al.*, 1993). Subsequently, a new scientific name, *Bemisia argentifolii* Bellows and Perring (Bellows *et al.*, 1994), and common name, the silverleaf whitefly, (Perring *et al.*, 1993) was proposed for strain B of *B. tabaci*. However, since the new scientific name has not been formally accepted by the Board of Zoological Nomenclature or the common name approved by the Entomological Society of America, the designations *B. tabaci*, strain B, and sweetpotato whitefly will be used in this review.

a. Biology/ecology on peanut. The sweetpotato whitefly has four nymphal instars on peanut, similar to its development on other hosts (Lynch and Simmons, 1993). However, each instar is smaller on peanut than on other hosts. This suggests that either peanut is not an optimum host or that the insect may not be fully adapted to peanut. Lynch and Simmons (1993) also noted that immature *B. tabaci* occurs on both the upper and lower leaf surfaces of peanut, which differs from their colonization of only the lower leaf surface of other hosts. This difference in colonization behavior of *B. tabaci* on peanut may be related to paraheliotrophism or to the thickness of the leaf lamina. Adult whiteflies are cryptic and rest on the underside of the leaves of most hosts. At night, peanut leaves fold upward and the lower leaf surface is more exposed than the upper surface. Thus, at night the upper leaf surface provides the more cryptic habitat for feeding and oviposition. Also, the length of the stylets of first-instar whiteflies average 80 mm (Pollard, 1955), while the thickness of leaf lamina averages 170 mm in runner cultivars of peanut (Kumari *et al.*, 1983) and the thickness of the leaf phloem is greatest in leaves below the penultimate leaf (Segovia and Brown, 1978). This means that first instars can easily reach the leaf phloem from either the upper or lower leaf surface of peanut.

Immature whiteflies are equally distributed among the tetrafoliolates of a peanut leaf (Lynch and Simmons, 1993), but their location on upper versus lower leaf surfaces varies over time (Lynch and Simmons, 1993; McAuslane *et al.*, 1993, 1994). Few immatures are found on the terminal or second leaf of a lateral branch of peanut. They are most abundant on leaves 3, 4, and 5, and then their abundance declined with increasing age of leaves. Adult whiteflies are most efficiently captured in peanut with yellow sticky traps placed in a horizontal position, at either the ground or canopy level, and with the sticky surface upward.

Damage to plants by the sweetpotato whitefly is through direct removal of photosynthate from the phloem and by the production of honeydew by immatures; honeydew excreted by nymphs drops to lower leaves and is colonized by sooty molds (e.g., *Capnodium* spp.). Sooty molds reduce light interception by leaves (Byrne *et al.*, 1990).

Bemisia tabaci poses a threat to peanut production in the U.S. because of its resistance to insecticides, occurrence on the underside of leaves where it is difficult to control, high intrinsic rate of increase on susceptible hosts, and, most importantly, its ability to transmit viral diseases to plants (Gerling, 1990b). At present, the sweetpotato whitefly is not adapted well to peanut (Lynch and Simmons, 1993), and no whitefly-borne viruses have been reported on peanut in the U.S. However, the sweetpotato whitefly can adapt to new hosts and become a major pest in only a few generations (van Lenteren and Noldus, 1990). Brown and Bird (1992) reported that "host specialization has been observed particularly with populations that were previously and/or continuously reared on a particular plant species under laboratory or field conditions".

Six or seven morphological classes of whitefly-transmitted viruses have been identified (Duffus, 1987), with the gemini viruses being the most

important. They are transmitted in a persistent-circulative manner by whiteflies. Brown and Bird (1992) listed 13 geminiviruses transmitted by whiteflies in North America and noted that endemic diseases are pandemic throughout the tropical Americas and the Caribbean Basin. This enhances the likelihood that viral strains may arise that will infect peanut.

A national research and action plan for the development of management and control strategies was initiated in 1992 because of the importance of the new strain of *B. tabaci* in the U.S. (Anonymous, 1992). The plan was developed through a cooperative effort among personnel at USDA-ARS, State Agricultural Experiment Stations, Animal and Plant Health Inspection Service, and the USDA Extension Service and identifies six major research priorities—(a) ecology, population dynamics, and dispersal; (b) basic research on systematics, biotypes, behavior, physiology, biochemistry, and vector-virus interactions; (c) control via biorationals, new chemicals and/or improved pesticide application technology; (d) biological control through conservation and determination of the effectiveness of indigenous natural enemies, importation on new natural enemies, and development of mass rearing techniques for the important natural enemies; (e) develop crop cultivars with resistance to the sweetpotato whitefly; and (f) determine crop management systems and host sequences that best manage whitefly populations.

b. Biological control. Research in Florida has recently identified several common parasitoids of the sweetpotato whitefly on peanut—*Encarsia nigricephala* Dozier, *E. pergrandiella* Howard, *E. transvena* (Timberlake), and *Eretocerus californicus* Howard (McAuslane *et al.*, 1993). *Encarsia nigricephala* was the most abundant species, accounting for 91% of the parasitoids collected in 1991 and 54-71% in 1992. Parasitized fourth instars are most abundant on leaves five to seven. Immature whiteflies occur on both the upper and lower leaf surfaces, but parasitized immatures occur most frequently on the lower surface. In subsequent years, these species were again the predominant parasitoids with *E. nigricephala* accounting for 53 and 85%, *E. transvena* 25.6 and 4.7%, and *E. pergandiella* 18.3 and 9.8% of all parasites reared from whiteflies in 1992 and 1993, respectively (McAuslane *et al.*, 1994). These authors noted that parasitism was extremely important in whitefly mortality especially late in the peanut growing season when 90 to 100% of all fourth instars on peanut in Florida were parasitized.

Research and quarantine facilities have been established at Weslaco and Mission, TX and at Stoneville, MS to receive imported natural enemies of the sweetpotato whitefly and to conduct basic biological studies on exotic natural enemies. Detailed reviews of the natural enemies of whiteflies were published by Gerling (1990a) and Fransen (1990).

c. Host plant resistance. Resistance in several species of plants to the sweetpotato whitefly has been reported (De Ponti *et al.*, 1990). However, the insect is a relatively new pest of peanut and little research has been done to identify sources of resistance. Preliminary observations revealed that the number of immature *B. tabaci* is only about one-quarter as great on the leaves of Southern Runner as on Florunner (R.E. Lynch, unpubl. data, 1993).

McAusline *et al.* (1994) also reported lower populations of *B. tabaci* on Southern Runner in 1992, but noted that in 1993 it contained the greatest population of immatures, except red-eyed nymphs, of all cultivars evaluated. Evaluation of peanut genotypes, including GP-NC 343 and crosses between GP-NC 343 and 81206 and 567A, failed to identify germplasm more resistant to the sweetpotato whitefly than the cultivars Southern Runner and Florunner (McAuslane, 1995).

FUTURE DIRECTION FOR PEANUT ENTOMOLOGY

Like other sciences, entomology has changed considerably during the past 10 years, and the rate of change is expected to escalate into the 21st century. In the foreseeable future, four areas of research will most likely have a tremendous impact on insect management in peanut. These include pest forecasting, genetic engineering, transferring resistance to insects found in the wild species of *Arachis* to cultivated peanut, and increased emphasis on biological control. The current philosophy in the U.S. on environmental pollution and the perception, be it real or imagined, that agricultural chemicals are used excessively in production of food and fiber has changed the direction of future research. However, the discovery of new techniques—such as moving a gene from one species to another and estimating the density of migrating insects with radar coupled with meteorological advances for tracking their movement—are equally important in the advancement of entomology. The importance of natural enemies in the management of peanut pests has been noted above and will not be discussed here, even though future directions in the way biological control is employed may change considerably in the next 10 years. An overview of the potential for the other three areas will be presented, since they are expected to have an even greater impact on entomology as well as the other sciences related to peanut.

Pest Forecasting and Prediction Models

The ability to forecast pest abundance will probably increase in coming years so that growers can be warned of potential economically damaging populations of pests before they actually occur. How will forecasting be done? There are several potential methods of forecasting the abundance of insect pests in peanuts—(a) using models to predict outbreaks, (b) forecasting with pheromone traps, (c) predicting movement of migratory insects, and (d) technological predictions.

Using Models to Predict Outbreaks. Decision support and simulation models are becoming more accurate and more realistic each year as computer power and knowledge of an agroecosystem improves. Such models offer tremendous potential for use in IPM systems by integrating the effects of various biotic and abiotic stresses (i.e., insect, plant pathogen, drought, etc.) on pest biology and/or crop physiology, yield, and quality. Systems, such as LCB-Days (Mack *et al.*, 1993), offer hope that pest outbreaks can be predicted in peanuts before major damage occurs. The abundance of many

species of arthropods in peanut fields is influenced by weather events, so algorithms that include weather variables will probably have an impact on predicting outbreaks in the future. Knowledge-based systems will probably increase in usage as growers become more computer literate. Knowledge-based systems are especially useful for decision-making since an expert system can both recommend a solution and display the reasoning used to reach the solution. The potential use of knowledge-based systems exists in all major field crops, especially those like peanut that have a relatively high profit margin. For example, COMAX is an expert system developed for assisting in cotton pest management (Lemmon, 1986). COMAX combined an expert system with a simulation model to make decisions about irrigation schedules and fertilizer recommendations.

Knowledge-based systems offer a great deal to pest managers. They can process qualitative information and make decisions, they can explain how they arrived at the decision, and the system is available for everyone's use at the same time (Plant and Stone, 1990). Further, the knowledge base can be edited and improved yearly with additional qualitative and quantitative information. Knowledge-based systems also may eventually supplant direct contact as the most common method of extending knowledge to growers.

Basic models will also assist in forecasting pests. Peanut plant growth and development have already been modeled (see Chapter 9), so coupling pest injury algorithms to the physiological plant models should occur in the near future. Such coupling will allow scientists to simulate damage to peanut under an almost endless number of scenarios, and should help to refine the economic injury levels for peanut pests.

Forecasting with Pheromone Traps. Insect pheromones may offer a means of forecasting pest abundance. The use of sex attractants combined with sticky traps has been studied extensively for several insects. Sridhar *et al.* (1988) found that the number of egg masses of *S. litura* is positively correlated with an increase in male capture in pheromone traps. Ranga Rao (1991) evaluated several pheromone combinations in different types of traps for capture of *S. litura* and recommended use of single-funnel traps that are currently being used in a national monitoring network for this pest in India. Pheromone traps also have been used for the corn earworm and fall armyworm (Westbrook and Sparks, 1986; Pair *et al.*, 1987; Lynch and Douce, 1992). In the U.S., Pair *et al.* (1987) related trap catches of the fall armyworm in its overwintering sites to winter weather conditions. Raulston *et al.* (1990) used pheromone traps to estimate abundance of corn earworm adults in corn fields in Texas. Brandenburg *et al.* (1992) attempted to use pheromone traps to relate adult male populations of the southern corn rootworm with damage to peanut pods in the field; the pheromone traps were only able to predict fields with a low potential for rootworm damage.

More information is needed, however, before pheromone traps can be successfully used to predict abundance of pests. It is critical to verify that pheromone traps accurately reflect the abundance of moths in the field. This requires that trap counts be compared with an absolute estimate of adult abundance, such as flush counts (Funderburk *et al.*, 1987; Mack and Backman,

1987). Comparisons must be made in both low and high densities of adults. One may expect pheromone traps to more accurately estimate the abundance of males when few females are present but to inaccurately estimate abundance of males when many females are present. This would mean that pheromone traps could not be used to estimate peak populations and, thus, negate much of their usefulness. Further, the synthetic pheromones may be more attractive to a particular age-class of males, such as newly emerged or older, nonreproductive males. This also would negate the usefulness of trapping. A comparison of age-class of males in pheromone traps versus males caught in the field would help answer this question.

Predicting Movement of Migratory Insects. The atmospheric transport of migrating insects is an emerging research area in entomology. An Alliance for Aerobiology Research has recently been formed (Isard, 1993), and a Southern Regional Information Exchange Group on Multinational Pest Management has been recently created. Both groups emphasize understanding how and when insects can travel long distances. In peanut and other crops, the long-distance movement of insects that are unable to overwinter at northern latitudes (e.g., the armyworm complex, aphids, thrips, and leafhoppers) is influenced by weather patterns. For example, Westbrook and Sparks (1986) used retrogressive atmospheric trajectories to target probable overwintering sites of the fall armyworm in the southeastern U.S. Pair *et al.* (1991) sieved soil in cornfields in northern Mexico through southern Texas to estimate the populations of fall armyworms that would emerge, used radar to estimate density of moths aloft on a passing weather front, calculated trajectories of the moths based on weather patterns and wind speed, and used pheromone traps to demonstrate immigration of moths on the weather front into the High Plains of Texas. This enabled them to demonstrate long-distance migration of the fall armyworm and illustrated the usefulness of such procedures for predicting movement of migratory insects. Dispersal of the *Helicoverpa* moths on weather fronts also has been studied in the U.S. (Sparks *et al.*, 1989; Wolf *et al.*, 1990), in the Middle East (Pedgley, 1986), and in Australia (Farrow and Daly, 1987). The development of predictive models based on insect abundance, predictive weather patterns, insect flight trajectories, and potential dispersal will prove useful in the management of insects and other pests.

Technological Predictions. New technology will almost certainly alter our ability to predict abundance of certain pests of peanut. We are currently in the 'information age', where humankind is being bombarded with more information than ever before. This new information will take many new and useful forms in the near future. LANDSAT and GOES satellite photographs depicting plant stress may be interpreted in real time in the future so that defoliation and water stress can be gauged (Pinter, 1982). If so, then density of migratory moths could be estimated from space. These data combined with real time weather data and a soils database would enable us to predict outbreaks of two important insects, the southern corn rootworm and lesser cornstalk borer. Soil data bases are now available on computer that have soil information in any given county in the U.S., with a cell size as small as 1 ha

(B. Hajek, pers. commun., 1993). This means that future models would be able to divide a grower's peanut field into many small cells and may predict abundance in each cell. Weather data will become more accessible and more accurate with the replacement of the 1950s technology weather radar units with the WSR-88D doppler radar units, as is currently occurring. These units will allow us to estimate from radar how much rainfall occurs in any given area. Such data will be linked to weather networks, such as the Oklahoma Mesonetwork (Dahlgren, 1991). This network is composed of a series of 107 computerized weather stations that monitors the weather every 15 min and sends information to a central computer for access by farmers and scientists.

Geographical Information Systems offers yet another untapped resource for predicting insect abundance (Isaaks and Srivastava, 1989). Entomologists are just beginning to use these systems (Williams *et al.*, 1992a). These systems can map infestations of insects on a large scale and may have uses for understanding infestations of peanut insects such as the lesser cornstalk borer and termites.

Many of these new technologies will probably alter the way that we currently do business. It is time that we begin preparing for these new technologies and applying them to entomology.

Resistance to Insects in the Wild Species of *Arachis*

Many of the wild ancestors of modern agricultural crops evolved defense mechanisms to limit damage by herbivores. Peanut is no exception to this axiom of plant resistance. Resistance has been identified in a large number of the wild species of peanut to pest arthropods such as the groundnut aphid, tobacco thrips, potato leafhopper, groundnut jassid, twospotted spider mite, fall armyworm, tobacco caterpillar, groundnut leafminer, lesser cornstalk borer, and jewell beetle (Table 8). The level of resistance in several instances is so high that many species of *Arachis* are essentially immune to attack by one or more insect pests and/or they do not support development or reproduction by the insect. Examples of *Arachis* spp. resistance to insect pests include *A. villosa*, *A. diogoi* (formerly *A. chacoensis*), and *A. glabrata* to *A. craccivora*; aphids which fed on plants of these species failed to reproduce or showed a drastically reduced rate of reproduction (Amin, 1985). Similarly, *A. villosa* and *A. burkartii* are highly resistant to the fall armyworm; larvae of the fall armyworm that were fed leaves of these species failed to complete larval development (Lynch *et al.*, 1981). Thus, excellent levels of resistance to some of the major arthropod pests of cultivated peanut that would prove very beneficial throughout the world are found in the wild species of *Arachis*.

However, the transfer of resistance found in wild species of *Arachis* to the cultivated peanut may be more difficult to accomplish than once believed. Polyploidy exists within the genus *Arachis*; most wild species are diploid ($2n = 2x = 20$), while three are tetraploid ($2n = 4x = 40$) (Smartt and Stalker, 1982). These authors suggested that polyploidy may have arisen independently twice in the evolution of peanut. Chromosome analyses suggest two structurally different genomes even within *A. hypogaea*, and possibly as

many as 11 distinct genomes among species of the different sections of the genus (see Stalker and Simpson, Chapter 2). Thus, use of genetic material within the section *Arachis*—i.e., the section with *A. hypogaea*—is likely to be more successful and predictable than the use of genetic material from more distant relatives of the cultivated peanut (Smartt and Stalker, 1982). Breeding strategies currently are being developed to transfer needed genetic material through interspecific crosses and more efficient manipulations of ploidy levels (Stalker, 1992). In other cases, genetic engineering to transfer a single dominant gene appears to be a logical solution (see Knauft and Ozias-Akins, Chapter 3). However, as noted by Smartt and Stalker (1982), the allopolyplodity nature of *A. hypogaea* may restrict expression of genetic material even when useful genes are introgressed from cross-compatible species. Thus, utilization of sources of resistance from species outside section *Arachis* is not currently possible.

Genetic Engineering In Peanut Entomology

Genetic engineering of plants by inserting foreign genes, from either alien species or clones within a species, that are deleterious to insects greatly enhances the potential for using host plant resistance for managing insect pests. The use of genetically engineered crops for managing insect pests has several potential advantages over the use of chemical control methods. These advantages include (a) independence from weather since the toxin is in the plant and cannot be washed off (the application also is not prevented due to inclement weather); (b) production of the toxin in plant parts that may not be accessible to chemical pesticides (i.e., roots, underside of a leaf, or new growth); (c) production of the toxin continuously so that it is present when the infestation occurs; (d) presence of the toxin when the insect first emerges and is most susceptible; (e) reduction in production costs since expensive application equipment, labor, and fuel are not required to apply the control agent; (f) decreased cost for genetically engineering a plant, now that techniques have been developed, compared with the >$65 million required to discover, evaluate, register, and produce a conventional insecticide (Hoy, 1992); (g) reduced concern for environmental contamination since the toxins are natural products and are biodegradable (however, EPA is now considering regulation of natural toxins); and (h) compatibility with other management tactics since the active ingredient is toxic only to phytophagous insects rather than to both pests and their natural enemies (Gatehouse *et al.*, 1991; Starnes *et al.*, 1993).

In addition, transfer of a single gene for resistance to an insect is faster with recombinant DNA technology than by conventional plant breeding. Recombinant DNA techniques allow modification of the gene before insertion, and insertion of the gene into high-yielding, commercially acceptable lines, without transfer of unwanted genetic material that often occurs in conventional plant breeding (CAST, 1986). Thus, the recombinant DNA technologies will have a major impact on agriculture and food production in the near future (CAST, 1986).

Peanut has only recently received attention from genetic engineers (see

Knauft and Ozias-Akins, Chapter 3). The need for genetic engineering for resistance to insects has been discussed among various peanut research groups, both from the standpoint of resistance to insects and possible reduction of aflatoxin contamination which is associated with pod damage by insects. A brief review of recombinant DNA research conducted on tomato (*Lycopersicon esculentum* Mill.), tobacco (*Nicotiana tabacum* L.), and cotton to insert genes for resistance to insects exemplifies the potential for such research on peanut.

Research on resistance to insects using genetic engineering has concentrated primarily on three areas: (a) transfer of genes for production of the δ-endotoxin(s) from *B. thuringiensis* to plants, (b) transfer of plant proteinase genes to other plant species, and (c) transfer of genes to baculoviruses to improve efficacy (Broadway *et al.*, 1986; CAST, 1986; Maeda, 1989; Boulter *et al.*, 1990; Gatehouse *et al.*, 1991).

***δ-Endotoxins from* Bacillus thuringiensis.** *Bacillus thuringiensis* is a common soil-inhabiting bacterium that has the unique ability to produce a crystalline protein during sporulation that is toxic to insects. Recently, Hofte and Whiteley (1989) reviewed the crystalline proteins produced by *B. thuringiensis* and proposed a new classification based on structural similarities and insecticidal activity. All of these proteins are protoxins and are proteolytically cleaved into toxic fragments in the insect gut. Many of these proteins, varying in homology of amino acid sequence and activity against insects, have been isolated from different subspecies of *B. thuringiensis*. Characterization of these proteins suggests that they are encoded by 14 distinct genes, 13 of which are considered a family of related insect toxins termed *Cry* proteins for their crystalline nature. The other gene produces a 27-kDa protein that is cytolytic to a variety of invertebrate and vertebrate cells and is unrelated to the *Cry* genes. The 13 *Cry* genes with insecticidal activity have been divided into four major groups— i.e., *CryI*, six different genes that encode 130- to 140-kDa proteins specific for Lepidoptera; *CryII*, two genes, both of which encode 65-kDa proteins with activity against Lepidoptera and Diptera; *CryIII*, a single gene that encodes a 72-kDa protein specific to Coleoptera; and *CryIV*, four genes that encode proteins of 72-, 78-, 128-, and 135-kDa with activity against Diptera.

The first research on the transfer of *CryIA(b)* and *CryIA(c)* genes to plants (Vaeck *et al.*, 1987; Fischhoff *et al.*, 1987) produced only moderate insect control because of their poor expression of their protein products in plants. Expression of toxic proteins in transgenic plants was enhanced by the use of an improved promoter, the 35S promoter of the cauliflower mosaic virus, in *Agrobacterium tumefaciens* and a truncated form of the gene for toxin production (Perlak *et al.*, 1991; Carozzi *et al.*, 1992; Jenkins *et al.*, 1993). These modifications led to the expression of insecticidal crystalline protein in leaves, corolla, calyx, anthers, pith, and roots of tobacco (Carozzi *et al.*, 1992) and reduced survival of *H. virescens* on cotyledons, seedling stems, first true leaves, terminal leaves, squares, and petals of transgenic cotton (Jenkins *et al.*, 1993). Recently, the *CryIA(b)* gene has been fused with the *PR-1a* gene from tobacco to form an inducible defense system that is

triggered by inoculation with pathogens or chemical stimuli (Williams *et al.*, 1992b). New isolates of *B. thuringiensis* producing *Cry*III proteins with activity against larvae and adults of the southern corn rootworm and other Coleoptera also have been reported (Slaney *et al.*, 1992; Johnson *et al.*, 1993). Other research has shown that transgenic plants containing genes for δ-endotoxin proteins do not adversely affect populations of natural enemies (Warren *et al.*, 1992; Wilson *et al.*, 1992).

The *CryIA(c)* gene has recently been transferred to peanut and evaluation of callus tissue showed a high level of toxicity to the lesser cornstalk borer (P. Ozias-Akins, C. Singsit, and R.E. Lynch, unpubl. data, 1994).

Plant Protease Inhibitor Genes. Protease inhibitors have been found in several species of plants. These proteins may normally be present in plant tissue (Boulter *et al.*, 1990; Gatehouse *et al.*, 1991), or they may be induced as a result of injury (Broadway *et al.*, 1986). When ingested by insects, protease inhibitors inhibit the activity of digestive enzymes, such as trypsin and chymotrypsin, resulting in improper digestion of proteins, starvation and death. The most promising of these protease inhibitors is the cowpea trypsin inhibitor (*CpTI*) from *Vigna unguiculata* L. (Boulter *et al.*, 1990; Hoffmann *et al.*, 1992). *CpTI* produces small polypeptides of about 80 amino acids. The gene for *CpTI* has been transferred to tobacco and has provided resistance to a wide range of insects among the Lepidoptera, Coleoptera, and Orthoptera. Protease inhibitors from tomato and potato also have been transferred to tobacco and enhance resistance to the tobacco hornworm, *Manduca sexta* (L.) (Johnson *et al.*, 1990). In addition to the protease inhibitors, other plant proteins such as lectins and amylase inhibitors show potential for genetic engineering to provide plant resistance to insects (Gatehouse *et al.*, 1990).

Baculoviruses. Baculoviruses are a group of DNA viruses that are pathogenic to insects, especially Lepidoptera, and include the nuclear polyhedrosis viruses, the granulosis viruses, and the nonoccluded baculoviruses (Blissard and Rohrmann, 1990). As a group, baculoviruses are pathogens of low virulence, requiring 3 to 10 days after their ingestion to kill an insect. However, they are very efficient in transporting their own double-stranded DNA into host cells; thus, they are ideal candidates as recipients or vectors of foreign genetic material (Maeda, 1989). Using recombinant DNA technology, the gene for δ-endotoxin production has been transferred to the nuclear polyhedrosis virus of the alfalfa looper, *Autographa californica* (Speyer), to improve its efficacy (Martens *et al.*, 1990; Merryweather *et al.*, 1990). Research also is underway to transfer genes for polypeptides that block neural function in insects and insect peptide hormones to baculoviruses (Maeda, 1989; Starnes *et al.*, 1993).

Insect Resistance to Genetically Engineered Toxins. Insects have an ability to rapidly overcome toxins in their environment by developing physiological/biochemical mechanisms that make them highly resistant to toxins. In 1987, it was estimated that over 400 species of insects are resistant to one or more insecticides and that this number doubles every 6 years (Rowe and Margaritis, 1987). Similar concerns have been expressed for the development of resistance in insects to the toxin(s) produced in genetically engineered plants (Rowe and Margaritis, 1987; Gould *et al.*, 1992; Williams

et al., 1992b). These concerns may well be justified since the rate at which resistance develops in insects is directly related with intensity of use of a toxin. This relationship for the development of resistance is just as applicable for resistance to insect toxins produced in genetically engineered plants as it is for resistance to conventional insecticides. Until recently, however, resistance to bioinsecticides such as *B. thuringiensis* was known only for laboratory populations of insects such as the Indian meal moth, *Plodia interpunctella* (Hübner) (McGaughey, 1985); the diamondback moth, *Pluetella xylostella* (L.) (Tabashnik *et al.*, 1990); and the tobacco budworm, *H. virescens* (Gould and Anderson, 1991). Tactics proposed to limit the rate at which resistance develops in insects to the toxin(s) produced by genetically engineered plants include (a) production of the toxin only in specific tissue rather than in the entire plant, (b) interplanting transgenic and nontransgenic plants, (c) production of the toxin only in response to a signal such as a specific developmental stage of the plant or to an environmental cue (e.g., insect feeding), (d) replacement of one toxin with another toxin as the insect becomes resistant to the original toxin, and (e) insertion of multiple toxins within the transgenic plant (Gould, 1988; Williams *et al.*, 1992b).

Two recent reports have added to the controversy over developing and managing insect resistance to toxins in transgenic plants. First, resistance to *B. thuringiensis* subsp. *kurstaki* in larvae of the diamondback moth collected from the field has been documented in several locations in the U.S. (Shelton *et al.*, 1993). The development of diamondback moth resistance is related to intensive use of *B. thuringiensis* applied via conventional techniques. The development of such resistance increases concerns about the rapid development of resistance and/or cross-resistance to the *B. thuringiensis* toxin(s) in transgenic plants. Secondly, cross-resistance to *B. thuringiensis* toxins that differ significantly in structure and insect activity was reported in *H. virescens* (Gould *et al.*, 1992). Thus, IPM strategy using toxins expressed in transgenic plants offers tremendous potential for improving agricultural production while reducing the use of conventional insecticides (Starnes *et al.*, 1993). However, like conventional pesticides, resistance in insects to genetically engineered toxin will continue to be a major concern in transgenic plants.

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