15

Potential role of pheromones in fire ant control

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Introduction

The black imported fire ant, *Solenopsis richteri* (Hymenoptera: Formicidae), was accidentally brought into the Mobile, Alabama area around the turn of the century. This was followed in the early 1930's by another Mobile, Alabama area introduction of the red imported fire ant, later described as *Solenopsis invicta* (Buren, 1972).*Solenopsis richteri* is believed to have originated from Argentina or Uruguay and *S. invicta* from Brazil. Imported fire ants currently infest over 250,000,000 acres of land in the southern United States and Puerto Rico. However, their potential range in the United States is much greater. The fire ant spreads through mating flights up to 6 miles a year, not enough to account for its current distribution. Man has been the main distributor of fire ants through shipments of nursery stock and other goods. Despite stringent state and federal quarantine efforts, there have been recent reports of incipient imported fire ant infestations in California, Arizona, Oklahoma, Virginia and Maryland.

The ants' potent sting, tremendous reproductive capacity and opportunistic, omnivorous behavior have made them a significant medical and agricultural pest. About one percent of the human population develop allergic reactions to fire ant stings, as is the case for honey bees. However, since many more people are stung by fire ants (about one third of the population in an infested area per year), there are more reports of hypersensitivity to their venom (Adams and Lofgren, 1981). While long-term residual chlorinated hydrocarbon insecticides were used in the 1950s and 1960s there were few reports of fire ant crop damage; however, prior to their use in the late 1940s and early 1950s and after their residual effects dissipated in the 1980s, it was apparent that fire ant infestations affected many crops (citrus, potatoes, soybeans, etc.).

Continued pressure from the public to reduce the amount of pesticides used in the United States is reflected in the attitude of the EPA. Recently, all insecticides registered

prior to 1984 were required to undergo re-registration. It is estimated that over 80 percent of the previously registered insecticides are no longer available. This places more emphasis on "biologicals", which include pheromones, and the specific targeting of available insecticides to the pest.

How can pheromones be used to control fire ants

Many behavioral responses in social insects are mediated by chemicals produced by the insects themselves. When this occurs the specific chemicals are called pheromones. Examples are pheromone mediation of alarm, attraction, nestmate recognition, recruitment, trail following, and control of competing reproductives. Many of these categories have been investigated over the past 30 years in the fire ant, as well as in other ant species.

Disruption of essential colony processes and functions

Pheromones are involved in many key elements of the social structure of the fire ant colony. For example, Dufour's gland products are responsible for recruitment to food sources in the foraging arena. The large fire ant colony populations (up to 250,000 workers) are the result of highly efficient foraging on the part of workers and the queen's very high egg-laying rate. Use of recruitment pheromones to disrupt recruitment activity could have serious effects on fire ant populations. Dufour's gland products also elicit colony migration and alarm. Artificial inducement of these behaviors would disrupt normal colony function. Other areas where interdiction with synthetic pheromones could be part of an integrated management scheme are mating flight activity, mate location, worker regulation of caste, and nestmate recognition.

Improvement of fire ant baits

Over the past two decades, insecticide baits have been developed for fire ant control. Baits have a distinct advantage over treatments that require direct or vapor contact with colony workers and the queen, because much less active ingredient is required for control. However, they do affect certain non-target organisms. The following premise is the basis for our approach to this problem:

> If *Solenopsis invicta* can be induced through the use of species-specific attractant pheromones to get to a bait toxicant before other ant species, then the bait will be more effective and at the same time there will be less hazard to non-target organisms.

Several advantages are inherent in the development of baits with enhanced species-specificity: A) The most serious natural enemies of fire ants are other ants that compete for territory and resources and, most importantly, take a toll on newly mated queens. Greater bait specificity means fewer negative effects on non-target ant species. If the fire ant could be eliminated from an area without affecting other ant species, then these species through competition and elimination of newly mated queens could significantly decrease the rate of reinfestation. B) Greater specificity means that more bait could reach the fire ant target; therefore, it may be possible to (1) use less bait per unit area; (2) decrease the amount of active ingredient in each bait particle; (3) decrease the percentage of phagostimulant (currently soybean oil) in each particle; or (4) decrease the percentage of both active ingredient and phagostimulant. C) Greater specificity and less active ingredient would promote species diversity and place a smaller insecticide load on the

environment, a desirable objective in view of ever-increasing public and government scrutiny of insecticide use.

What are the pheromone possibilities?

The following summarizes what is currently known about fire ant pheromones and how they might be used in integrated management of the fire ant.

Queen-produced pheromones

Queen-produced pheromones control essential colony processes for many ant species (Hölldobler and Wilson, 1983; Brian *et al.*, 1981), and the fire ant is no exception (Vargo and Fletcher, 1986). Several queen-produced pheromones are known to exist; however, our knowledge of their function, source and chemistry varies considerably. They all share possibilities for providing innovative ways to control fire ant populations.

Caste differentiation

Caste differentiation is an essential element of social insect colony organization (Wilson, 1985). In fire ant colonies there are two female castes, reproductive females (queens) and sterile female workers. Depending on the time of year, winged female (virgin) reproductives may exist in the same colony as the inseminated queen(s). There are no distinct morphological castes among fire ant workers, although age and size related polyethism does occur (Mirenda and Vinson, 1981). Queen/worker differentiation is a temporal arrangement of a combination of inhibitory and facilitatory factors acting on queen development (Wheeler, 1986). The production of workers is considered a deviation from normal female reproductive development. There are two general processes by which caste differentiation can occur: queen-controlled caste determination and worker-controlled caste regulation.

Caste determination.   Caste determination is achieved by the queen through deposition of eggs with potential for developing into either queens or workers. This can occur at any point from vitellogenesis through embryogenesis via hormonal effects (juvenile hormones, ecdysteroids, and neuropeptides). It is known that when fed to a colony, juvenile hormone analogues act only on eggs or very young larvae to produce intercastes and female alates (Robeau and Vinson, 1976). Many compounds isolated and identified from the Dufour's gland of ants, including fire ants, are very similar to insect juvenile hormones (JH) and may have JH activity (Feyereisen *et al.*, 1981). Most interesting for caste determination in fire ants is that the queen's sting apparatus is intimately involved in oviposition (Vander Meer and Morel, 1995). This, coupled with a queen's muscular control over release of compounds from both her poison and Dufour's glands (Billen, 1990), suggests that caste determination could be affected during the egg-laying process through deposition of exocrine gland-produced pheromones on eggs as they are laid. This hypothesis remains to be investigated; however, the possibility for using these chemicals for colony control exists.

After colony foundation, a fire ant colony cycles through annual ergonomic (worker buildup) and reproductive (sexual production) phases (Oster and Wilson, 1978; Tschinkel, 1988). Interference with this natural cycle by artificially inducing a colony to produce

workers or sexuals at the wrong time would at least stress the colony and perhaps make it more susceptible to conventional control methods.

Caste regulation.   Caste regulation in social insects is carried out by workers under "queen control" (Fletcher, 1986). This regulation is accomplished by regulation of either the production or functioning of new sexual forms within a colony. For example, when queens of Pharaoh's ant, *Monomorium pharaonis* (L.), have a high egg production rate, only worker brood are reared; however, if egg numbers decrease, workers respond by rearing male and female sexuals (Edwards, 1987). Workers assess the quantity of eggs in a colony (queen fecundity), most likely through pheromones on the egg surface.

The situation in polygyne *S. invicta* colonies is analogous, except that in this case, the number of queens present in a colony influences the behavior of workers toward sexual brood. Vargo and Fletcher (1986) found that colonies with many queens did not produce sexuals, whereas polygyne colonies made queenless or allowed only one queen produced hundreds of sexuals. Daily addition of functional queen corpses inhibited sexual development, but virgin queens had no effect. Thus fire ant queens produce a pheromone that, if in high enough concentration, elicits worker behavior that is deleterious to developing sexual larvae. Vargo (1990) postulates that in response to the pheromone, workers restrict the food flow to female larvae so their development is shifted toward worker adults. Since male larvae have no alternative route, they are killed. In addition, workers may kill last-instar larvae of both sexes, because females sexuals at this stage cannot be diverted to workers.

This pheromone must be isolated, identified and made available through synthesis before its potential in fire ant control strategies can be evaluated. It is easy to envision the controlled release of this pheromone into fire ant colonies, with the effect of shutting down the fire ant's huge reproductive potential, especially in monogyne populations.

Dealation inhibitory primer pheromone

A mature fire ant colony can produce 5,000 or more winged female sexuals (female alates) a year. These sexuals will leave their home nest on mating flights in search of males. After insemination, many physiological changes occur in the queen; e.g. dealation (loss of wings), wing muscle histolysis, ovariole development, pheromone production, and commencement of oviposition. These same physiological changes occur without insemination in a female sexual through dealation, the loss of an alate's wings (Glancey *et al.*, 1981). Fletcher and Blum (1981) discovered that the colony queen produces a pheromone that inhibits the dealation process. Because the behavior is not immediately released by this pheromone it is classified as a "primer" pheromone. Production of this pheromone prevents female alates from competing with the queen for colony resources. If the queen of a colony dies, the alates present will dealate and start to produce all the pheromones associated with queens. They will also produce unfertilized eggs, which develop into males. Eventually the colony dies through natural worker attrition.

Fletcher and Blum (1981) postulated that workers accept only certain levels of queen pheromones. They observed that in orphaned colonies alate dealation began within 24 hours and that a few days later workers started to kill some of the dealates until only a few were left. Thus it appears that a pheromone excess prompts workers to eliminate the source until tolerable levels are again reached. From a practical point of view, high doses of these queen pheromones could be introduced into a normal colony, which theoretically

would induce workers to execute their own queen. Unfortunately, at the present time we do not know the source of the dealation inhibitory primer pheromone, nor its chemistry. Therefore, more research must be done on this system before it can be evaluated.

Queen attractant pheromone

The fire ant queen produces a pheromone in her poison gland that is highly attractive to workers (Vander Meer *et al.*, 1980). She has control over the release of this pheromone through the sting apparatus. Three components have been isolated from extracted queens that elicit a wide variety of worker behaviors, including attraction (Glancey *et al.*, 1983). These compounds (Fig. 1) have been identified and synthesized (Rocca *et al.*, 1983a,b). Two components (B and C) are optically active and the two enantiomers of each are available for evaluation (Mori and Nakazono, 1986a,b).
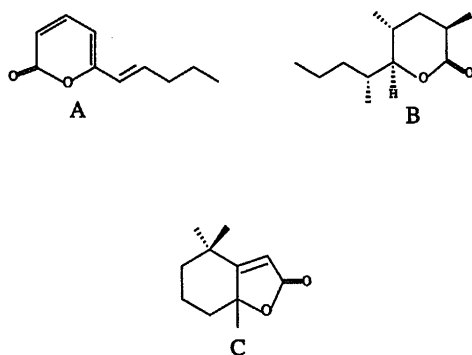

Figure 1. Fire ant queen pheromone components: A = (E)-6-(1-pentyl)-2H-pyran-2-one; B = invictolide; C = dihydroactinidiolide (Rocca *et al.*, 1983a,b).

The bioassays used to isolate the three components were not behavior specific. Since for bait enhancement a fire ant-specific attractant is required, the five synthetic components and the two racemic mixtures (A, –B, +B, ±B, –C, +C and ±C) were evaluated in an olfactometer (Vander Meer *et al.*, 1988) that measured worker response to volatiles in an air stream.

Five of the nine possible three-component mixtures were significantly attractive when presented to the ants at one queen equivalent (for optically pure B or C – 1ng A: 4ng B: 1ng C; for racemic ±B or ±C – 1ng A: 8ng B and 2ng C). From a commercial point of view A + (±)B + (±)C is the most desirable of the active three-component mixtures, since it is not necessary to synthesize costly optically pure compounds.

However, a two-component system would be even better; therefore we evaluated the 15 possible two-component combinations. Three mixtures showed significant activity. Two of these, (–)B + (–)C and (±)B + (–)C had undesirable high standard deviations, indicative of borderline activity. In contrast, A + (±)B demonstrated good attraction and consistent results. In fact, results for A + (±)B were better than those for the three-component system, A + (±)B + (±)C. In terms of future commercialization, our choice would be the less complicated two-component mixture rather than the three-component mixture.

Although reducing the number of components from three to two and determining that

optically pure components are not necessary was a big step forward, another important question deals with the concentration/activity profile. Ideally, we want significant activity over as broad a concentration range as possible, because if the activity range is narrow, it will be difficult to formulate the material with the correct release rate.

Results of activity/concentration studies for the two-component [A + (±)B] pheromone systems indicated significant activity in the olfactometer over a concentration range of two orders of magnitude. Future studies will determine if this will allow simple formulation or require more complicated controlled release technology.

At one queen equivalent there were no active single components. However, at elevated concentrations, component (±)B showed excellent activity over about one and a half orders of magnitude. This is an important result, because it may now be possible to work with only a single racemic compound. This greatly enhances the potential for developing a commercially viable species-specific bait using queen pheromone components.

Work is in progress through a USDA Cooperative Research and Development Agreement with American Cyanamid Company to evaluate the pheromone mixtures on bait particles.

Worker-derived pheromones

Recruitment pheromone

One of the reasons the fire ant is so successful is its highly efficient foraging strategy. It is composed of the following elements: 1. Solitary workers hunting for food move away from the nest in irregular looping patterns. 2. A worker locates food source and inspects it. 3. If the food source is large, the worker returns to the nest laying a chemical trail. 4. At the nest, additional workers are recruited and follow the chemical trail to the food. 5. Additional foragers reinforce the trail. 6. When the food is gone, the trail is no longer reinforced and the volatile chemicals dissipate (Wilson, 1962).

The fire ant recruitment pheromone chemistry and associated behaviors have been studied extensively. The source of the pheromone is Dufour's gland, which is attached to the base of the sting apparatus (Wilson, 1959). A worker makes a trail by releasing the Dufour's gland contents through the sting, which is periodically touched to the surface on which it is walking. We have reduced the recruitment process to three sub-categories: attraction, orientation induction, and trail following (Vander Meer *et al.*, 1981, 1988, 1990a). Workers are extremely sensitive to the pheromones. For example, one teaspoon of the orientation (trail following) pheromone, Z,E-alpha-farnesene, is enough to apply a 2 mm wide trail around the world over 5,000 times. We have also isolated the powerful pheromone components responsible for worker attraction (Vander Meer *et al.*, 1988): one of the two components must still be fully identified and synthesized.

The recruitment pheromones have control potential in several areas. The attractive part of the recruitment pheromone may be useful in enhancing the effectiveness of toxic baits, as discussed for the queen attractant pheromone. When Dufour's gland products are released by an individual not following a trail (non-recruitment context), colony migration or alarm may be elicited (Wilson, 1962). Thus, introduction of the recruitment pheromone into a colony at high concentrations could disrupt the colony's social structure and provide a non-insecticidal method of control. The utility of the recruitment pheromone in integrated management of the fire ant awaits the availability of the compounds through synthesis.

Nestmate recognition

Nestmate recognition occurs when a resident ant evaluates the odor of a potential intruder via its antennae. If the intruder smells like the resident no aggression occurs, but the intruder is attacked if it is sensed as being different. In fire ants, the recognition chemicals are derived from both environmental (soil, food, etc.) and heritable sources (Obin, 1986). Since in a given colony, odors are distributed uniformly among colony members through social interactions, each colony has approximately a uniform chemical profile. Also, because there is variability in the environmental and heritable cues, no colony has exactly the same chemical profile. Nestmate recognition is the first line of defense for the ant. Once an intruder is recognized as a non-nestmate, a host of chemical and behavioral defensive events are activated. An understanding of the recognition process may allow us to devise methods to "sneak" insecticides and/or pathogens into a fire ant colony without triggering the ants' defenses. We have gained a lot of knowledge about fire ant nestmate recognition; however, the chemistry involved is still to be elucidated (Vander Meer*et al.*, 1990b).

Fire ants had been thought of as having only one queen per nest (monogyny); however, the reality of the situation in the United States today is that we have increasing populations of multiple-queen fire ant nests (polygyny) (Glancey *et al.*, 1987). In monogynous populations, each nest is discrete and the workers from one nest are aggressive toward workers from other nests. We have found the opposite to be true for polygynous populations. Here each nest can contain hundreds of queens and the workers from one nest accept workers from other nests as nestmates, even if they are from monogynous colonies! This supports the idea that polygynous populations are acting as huge supercolonies, with free exchange of queens and workers (Morel *et al.*, 1990).

Polygynous populations have been empirically shown to be more difficult to control than monogynous colonies (Drees and Vinson, 1990). We have developed a simple aggression bioassay that readily identifies a population as to type with 100% accuracy with minimum nest disturbance (Morel *et al.*, 1990). Introduction of a polygyne intruder into a standard polygyne resident colony results in no aggression, whereas introduction of a monogyne intruder into a polygyne resident colony results in aggression initiated by the monogyne intruder. This assay will aid both future research and control of polygynous populations. The chemistry of fire ant nestmate recognition cues is unknown; however, they have potential in making toxic baits more acceptable, and in disrupting the social harmony of a colony, especially in polygynous populations. In addition, intraspecific aggression bioassay results are significantly different from interspecific results; therefore, the bioassay may help sort out complex fire ant taxonomic problems both here and in South America.

There are many fire ant parasites that live happily within the nest (myrmecophiles) and are unmolested by the normally aggressive fire ant workers. We have investigated how these parasites integrate into the host colony. In general, the parasites have a mechanism for surviving in the nest long enough to acquire, through interactions with the ants and the nest soil, the nestmate recognition cues of their host colony. For instance, *Martinezia duterteri* Chalumeau [=*Myrmecaphodius excavaticollis* (Blanchard)], a beetle that feeds on fire ant larvae, has an armored exoskeleton and plays dead when attacked. After about 24 hours in the host nest the beetle has acquired its host odor and is no longer attacked (Vander Meer and Wojcik, 1982). In another case, the tiny first-instar larva of a eucharitid parasitic wasp enters a fire ant nest undetected due to its small size. It, also, passively

acquires its host colony odor (Vander Meer *et al.*, 1989). There is a lot more to learn about parasite/host interactions, but our understanding of how they integrate into fire ant colonies should increase the probability for successfully using these parasites as biocontrol agents for fire ants. There are many other examples of fire ant myrmecophiles. All of these insects have evolved ways to brake through fire ant defenses and may serve as carriers for fire ant pathogens.

Alarm pheromone

Alarm pheromones have been reported in fire ants for almost 30 years (Wilson, 1962). Two sources have been postulated: Dufour's gland and a glandular source in the head. If the head-derived material is analogous to alarm pheromones from other ant species, the source is probably the mandibular gland. Research on Dufour's gland has focused on recruitment activity (Vander Meer, 1986), and work on the mandibular gland has been inhibited by the fact that it is composed of only a few secretory cells. Thus, no detailed behavioral and chemical work has been done yet on these pheromones. The potential of alarm pheromones in control is that they elevate workers to a heightened state of awareness and movement, resulting in quicker location of a bait particle than otherwise possible. Another approach is to use the material to disrupt normal colony function.

Brood-produced pheromones

Brood pheromones in ants have been the subject of many papers. A recent critical review of brood pheromones indicates inadequacies in the demonstration of their existence (Morel and Vander Meer, 1988). The fact that interspecific brood adoption readily occurs places the special brood/worker interactions (attraction, aggregation, and brood-tending) out of the pheromone definition. Instead, as postulated by Morel and Vander Meer (1988), brood/worker interactions may be mediated by a combination of associative learning, absence of aggressive behaviors, and nestmate recognition cues. Thus, the chemical part of this proposed hypothesis falls into the broad category of semiochemicals. I do not want to dismiss categorically the possibility of "brood pheromones", but offer a plausible alternative. This is a very interesting and complicated research area that has integrated management potential, but we are far from understanding this system.

   In related work, LaMon and Topoff (1985) studied the involvement of pheromones in the social facilitation of eclosion in *S. invicta*. Workers are attracted to eclosing pupae and aid the eclosion process by stripping away the pupal skin. The probability of successful eclosion is low without worker assistance. The chemicals responsible have not been isolated or identified; however, they offer potential in both bait enhancement and disruption of an important colony function.

Conclusion

Although we have a much better understanding of fire ant behavior, biochemistry and physiology then we did 15 years ago, there are many important gaps in our knowledge. For example, very little is known about what initiates mating flights, what causes the frenzied activity during the flights, and where and how the two sexes locate each other 100 to 200 meters up in the air. The mechanism of caste determination and regulation in fire ants is virtually unknown. Research in all areas of fire ant control represents the

cutting edge of social insect management. The successes achieved often find direct applications to the control of other social insects, especially other pest ants. Although the USDA is concentrating its effort on pheromone enhancement of currently available baits, little research is being done to evaluate the effects of pheromones on the social structure of the colony itself. "The challenge of deciphering the role of chemical mediators and devising effective approaches for their employment will require zeal, innovativeness, persistence, and long-term monetary investments. The result will be precise, specific, ecologically sound, and effective techniques essential for dealing with the pest control problems of the future" (Lewis, 1981).

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