EVALUATION OF POPULATION SUPPRESSION BY IRRADIATED LEPIDOPTERA AND THEIR PROGENY

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Lepidopteran species are among the most important pests of major annual and perennial crops, forests, and stored products throughout the world. More than 25% of the species that appear on a list of the 300 most important exotic insects that threaten the United States are in the order Lepidoptera (ESA 2001). In a supplement to that list, where the 30 most serious threats to Agriculture are named, 50% of the species are lepidopterans (ESA 2001). Unfortunately, control of lepidopteran pests worldwide is achieved almost entirely through the use of synthetic insecticides. This dependence on insecticides has contributed to the development of insecticide resistance in many of the most serious pests. Relevant examples include the codling moth, *Cydia pomonella* (Lepidoptera: Tortricidae) (Varela et al. 1993) and the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae) (Shelton et al. 1993), where resistance has developed even against the microbial insecticide *Bacillus thuringiensis* (Tabashnick et al. 1990). Heavy reliance and frequent indiscriminant use of pesticides also has had a significant negative impact on the environment. Of particular importance to agriculture is the destruction of crop pollinators and natural enemies that keep secondary pests in check (Edwards 2000). Development of alternative tactics to the unilateral use of insecticides is a major emphasis of most local, national and international research organizations concerned with pest control.

The Sterile Insect Technique and Lepidoptera

Genetic pest suppression is unique among biological methods in that it involves the release of genetically modified insects to control the same species (LaChance 1985). Sterile Insect Technique (SIT) programs have been quite successful against a number of pest Diptera (including the screwworm fly, *Cochliomyia hominivorax*, and the Mediterranean fruit fly, *Ceratitis capitata*), and numerous mass rearing facilities have been constructed worldwide to support these programs. However, compared to dipterans, lepidopterans generally are more expensive to rear and have a propensity to fly greater distances. Additionally, lepidopterans are more resistant to the effects of ionizing radiation than dipterans. As a consequence, the greater amount of radiation required to completely sterilize lepidopterans negatively impacts their competitiveness and performance in the field. Nevertheless, two SIT programs are currently operating against pest Lepidoptera, namely the pink bollworm, *Pectinophora gossypiella* (Saunders), program in the USA (Staten et al. 1993), and the codling moth program in Canada (Dyck et al. 1993; Bloem & Bloem 2000), and both of these programs have been very successful.

One approach to reduce the negative effects of radio-resistance in Lepidoptera has been the use of inherited or F_1 sterility. Proverbs & Newton (1962) first documented F_1 sterility during the course of their studies on the codling moth. Subsequently, investigators have reported F_1 sterility in many lepidopteran species of economic importance (LaChance 1985). Like SIT, F_1 sterility involves the mass rearing and release of genetically altered insects to insure that when matings occur in the field, a significant proportion of matings involve a treated, released insect. However, F_1 sterility takes advantage of two unique genetic phenomena in Lepidoptera. First, lepidopteran females generally are much more sensitive to radiation than are males of the same species. This may allow the dose of radiation to be adjusted so that treated females are completely sterile and males are partially sterile. Second, when these partially sterile males mate with fertile females the radiation-induced deleterious effects are inherited by the F_1 generation. As a result, egg hatch is reduced and the resulting (F_1) offspring are both highly sterile and predominately male. The lower dose of radiation used in F_1 sterility increases the quality and competitiveness of the released insects (North 1975). In addition, because F_1 sterile progeny are produced in the field, the release of partially sterile insects offers greater suppressive potential than the release of fully sterile insects (LaChance 1985) and is more compatible with other pest control mechanisms or strategies (Carpenter 1993).

Knipling (1970) explored the theoretical application of F_1 sterility for control of lepidopteran pests. Using mathematical models, he suggested that when releasing partially sterile insects, the sterile-to-wild overflooding ratio could be as low as ¼ of what is normally required for fully sterile insects. Population models developed by other researchers using data collected from several pest species (Carpenter 1993; Anisimov 1998) corroborate Knipling's findings.

Field releases of partially sterile insects have demonstrated the potential of using F_1 sterility to control many lepidopterans, including the cabbage looper, *Trichoplusia ni* (North & Holt 1969), the corn earworm, *Helicoverpa zea* (Carpenter et al. 1987; Carpenter & Gross 1993), the gypsy moth, *Lymantria dispar* (Mastro 1993) and the codling moth, *Cydia pomonella* (Proverbs et al. 1978; Bloem et al. 1999b; Bloem et al. 2001). In addition, many studies have shown that F_1 sterility can be effectively combined with other biological controls such as pheromone disruption (Bloem et al. 2001), entomopathogens (Hamm & Carpenter 1997), host plant resistance (Carpenter & Wiseman 1992a, b) and natural enemies (Carpenter et al. 1996; Greany & Carpenter 1999). As a result of these many studies, F_1 sterility is regarded as the most favorable genetic method for most applications against Lepidoptera (for a review, see Carpenter & Bartlett 1999).

The FAO/IAEA Sponsored Coordinated Research Programs (CRP's)

The Joint Division of Nuclear Techniques in Food and Agriculture of the Food and Agriculture Organization (FAO) and the International Atomic Energy Agency (IAEA) promotes agricultural development through the peaceful use of atomic energy. This mission is accomplished through their Technical Cooperation Projects, Coordinated Research Projects, publications, and meetings and training courses. In response to the recommendations of a group of consultants that met at the IAEA in Vienna in 1984, the Insect and Pest Control sub-program of the Joint FAO/IAEA Division designed and initiated the first five-year (1987-1991) Coordinated Research Program (CRP) on "Radiation Induced F_1 Sterility in Lepidoptera for Area-Wide Control." Research by CRP participating scientists focused largely on modeling the effects of releasing partially sterile moths on the field dynamics of feral populations, conducting laboratory studies to evaluate the relationship between radiation dose and sterility and conducting selected field-cage evaluations. Scientists from ten countries participated in this CRP, and the research results were published by the IAEA in 1993 (Anonymous 1993). As a result of the research progress during the CRP, the participants recommended to the FAO/IAEA that a second Coordinated Research Program should be considered which would emphasize field applications of inherited or F_1 sterility for lepidopteran pests.

A second CRP entitled "Evaluation of Population Suppression by Irradiated Lepidoptera and Their Progeny" was therefore initiated in 1995 with the objective of assessing the potential for controlling populations of pest Lepidoptera by releasing irradiated moths and/or their progeny in combination with other biological control methods. This CRP concluded in 1998. During this time period, three Research Coordination Meetings (RCM) were held to allow participants to discuss initial results and share ideas. The first RCM was held in Jakarta, Indonesia (24-28 April, 1995), the second meeting was held in Vienna, Austria (2-6 September, 1996), and the final meeting was held in Penang, Malaysia (28 May-2 June, 1998) in conjunction with the FAO/IAEA International Conference on "Area-Wide Control of Insect Pests Integrating The Sterile Insect and Related Nuclear and Other Techniques."

Twenty-five scientific teams from twenty-two different countries (Bangladesh, China, Pakistan, Myanmar, Syria, India, Java, Philippines, Mauritius, Vietnam, Tunisia, Bulgaria, Romania, Czech Republic, Russia, Ukraine, Iran, Austria, United States, Brazil, Cuba and Canada) participated in this second CRP. Participants conducted research on important pests of annual and perennial crops and stored-product pests (see Tables 1 and 2). The research findings have been published in three separate venues: as refereed publications in scientific journals, as part of a Technical Document or meeting proceedings published by the International Atomic Energy Agency, and as a block of four manuscripts following this introductory article. The manuscripts in this volume report important research findings from four different countries and on four different species. Ocampo (2001) describes the effects of a substerilizing dose of gamma radiation (100 Gy) on the mating competitiveness and mating propensity of the Old World cotton bollworm, *Helicoverpa armigera*, in the Philippines. Seth & Sharma (2001b) report on the effects of different doses of radiation on the common cutworm, *Spodoptera litura* reared on two different diets in India. Koudelova & Cook (2001) examine the competitiveness of mutant and irradiated males of the Mediterranean flour moth, *Ephestia kuehniella*, in the laboratory by counting eupyrene (fertile) and apyrene (non-fertile) sperm transferred to the female during copulation. Finally, Nguyen Thi & Nguyen Thanh (2001) report on the potential of combining F_1 sterility and the parasitoid *Cotesia plutellae* in a system to manage the diamondback moth, *Plutella xylostella*, in Vietnam.

Major Findings and Impact of the Research Conducted During the F_1 Sterility CRP

The research conducted during this CRP revealed principles that were common to all species studied. These can be summarized into two major points: (1) F_1 sterility is an effective and environmentally safe tactic for lepidopteran pest suppression that is useful under a variety of environments and crop production strategies. (2) F_1 sterility is compatible with all pest control tactics. The combination of F_1 sterility with pheromones, natural enemies, host plant resistance, entomopathogens and insecticides results in synergistic pest population suppression.

TABLE 1. LISTING OF THE SPECIES OF LEPIDOPTERA INVESTIGATED BY PARTICIPANTS OF THE FAO/IAEA RESEARCH COORDINATED PROGRAM ON EVALUATION OF POPULATION SUPPRESSION BY IRRADIATED LEPIDOPTERA AND THEIR PROGENY.

Family	Species	Common name	Crop	Reference
Noctuidae	*Spodoptera litura*	Common cutworm or Tobacco caterpillar	Soybeans, sorghum, corn, vegetables	Seth et al. 1997 Seth & Sharma 2001a, b
	Spodoptera exigua	Beet armyworm	Cotton, vegetables	Carpenter et al. 1996
	Spodoptera frugiperda	Fall armyworm	Forage grass, corn	Carpenter et al. 1997 Proshold et al. 1998 Arthur et al. 2001
	Helicoverpa armigera	Corn earworm or Cotton bollworm (Old World)	Corn, cotton, tomato	Pham Van et al. 1996 Ocampo et al. 2000 Rimas et al. 2000 Ocampo 2001 Lu et al. 2001 Ocampo & deLeon 2001
	Helicoverpa zea	Corn earworm	Corn, cotton, tomato	Mannion et al. 1995 Hamm & Carpenter 1997 Proshold et al. 1998
Gelechiidae	*Pectinophora gossypiella*	Pink bollworm	Cotton	Ahmad et al. 2001a, b
	Diatraea saccharalis	Sugarcane borer	Sugarcane	Garcia & Garcia 1996 Arthur et al. 2001
Tortricidae	*Cydia pomonella*	Codling moth	Pome fruit, walnut	Anisimov & Shvedov 1996 Chernyi et al. 1996 Bloem et al. 1999a, b, 2001 Mansour 2001
	Cydia molesta	Oriental fruit moth	Stone & pome fruit	Genchev 1996, 2001
Pyralidae	*Ectomyelois ceratoniae*	Carob or date moth	Date, carob, pomegranate	Dhouibi & Abderahmane 2001
	Ephestia kuehniella	Mediterranean flour moth	Stored grain	Matolin & Marec 1998 Marec et al. 1999 Koudelova & Cook 2001
	Crocidolomia binotalis	Cabbage webworm	Crucifer vegetables	Sutrisno Apu 2001
	Chilo suppressalis	Asian rice stem borer	Rice	Esmaili et al. 1996
Crambidae	*Ostrinia furnacalis*	Asian corn borer	Corn	Wang et al. 2001
	Ostrinia nubilalis	European corn borer	Corn	Chernyi et al. 1996 Rosca & Barbulescu 1996
Plutellidae	*Plutella xylostella*	Diamondback moth	Crucifer vegetables	Dunhawoor 1996 Okine et al. 1998 Mitchell et al. 1999 Nguyen Thi & Nguyen Thanh 2001 Sutrisno Apu 2001 Yang et al. 2001 Maung 2001
Arctiidae	*Spilosoma obliqua*	Hairy jute caterpillar	Jute	Rahman et al. 2001

This CRP also highlighted several areas that would benefit from further research and development to increase the economic viability of F_1 sterility programs. Development of diets using locally available ingredients would reduce rearing costs, especially in locations with developing economies. Improvements in mass rearing are needed to take advantage of the economy of scale as evidenced in dipteran SIT programs. Development of genetic sexing techniques, especially those that would eliminate females at the egg or early larval stage, would reduce rearing costs, would increase the efficiency of rearing, irradiation and release by 100% and would eliminate assortative mating of released moths in the field.

The FAO/IAEA sponsored CPR's have had major impacts in the direction of future research for the control of lepidopteran pests. For example, expanded research and implementation programs on F_1 sterility in combination with natural ene-

TABLE 2. LISTING OF THE TYPE OF STUDIES CONDUCTED AND SPECIES INVESTIGATED BY PARTICIPANTS DURING THE FAO/IAEA RESEARCH COORDINATED PROGRAM ON EVALUATION OF POPULATION SUPPRESSION BY IRRADIATED LEPIDOPTERA AND THEIR PROGENY.

Type of Study	Species and Reference
Diet Development and Insect Rearing	*Chilo suppressalis* (Esmaili et al. 1996) *Cydia molesta* (Genchev 2001) *Helicoverpa armigera* (Lu et al. 2001; Ocampo et al. 2000, Pham Van 1996) *Pectinophora gossypiella* (Ahmad et al. 2001b) *Spilosoma obliqua* (Rahman et al. 2001) *Spodoptera litura* (Seth & Sharma 2001a)
Radiation Biology	*Cydia pomonella* (Chernyi et al. 1996; Bloem et al. 1999a; Mansour 2001) *Diatraea saccharalis* (Arthur et al. 2001) *Ectomyelois ceratoniae* (Dhouibi & Abderahmane 2001) *Helicoverpa armigera* (Lu et al. 2001; Ocampo & de Leon 2001) *Ostrinia nubilalis* (Chernyi et al. 1996) *Pectinophora gossypiella* (Ahmad et al. 2001b) *Plutella xylostella* (Nguyen Thi & Nguyen Thanh 2001) *Spilosoma obliqua* (Rahman et al. 2001) *Spodoptera frugiperda* (Arthur et al. 2001) *Spodoptera litura* (Seth et al. 1997; Seth & Sharma 2001b)
Genetics and Genetic Sexing	*Ephestia kuehniella* (Koudelova & Cook 2001; Marec 1998; Marec et al. 1999; Matolin & Marec 1998)
Effects of Radiation on Sperm Development and Sperm Competitiveness	*Helicoverpa armigera* (Rimas et al. 2000) *Ostrinia furnacalis* (Wang et al. 2001) *Spodoptera frugiperda* (Carpenter et al. 1997)
Mating Competitiveness of Irradiated Insects and Their Progeny	*Cydia pomonella* (Bloem et al. 1999b, Mansour 2001) *Cydia molesta* (Genchev 1996) *Crocidolomia binotalis* (Sutrisno Apu 2001) *Diatraea saccharalis* (Garcia & Garcia 1996) *Helicoverpa armigera* (Ocampo 2001) *Ostrinia furnacalis* (Wang et al. 2001) *Plutella xylostella* (Nguyen Thi & Nguyen Thanh 2001; Sutrisno Apu 2001; Yang et al. 2001)
Compatibility of F_1 Sterility with Other Control Strategies	*Cydia pomonella* (Bloem et al. 2001) *Helicoverpa zea* (Hamm & Carpenter 1997; Mannion et al. 1995) *Pectinophora gossypiella* (Ahmad et al. 2001a, b) *Plutella xylostella* (Sutrisno Apu 2001; Maung 2001; Okine et al. 1998; Dunhawoor 1996) *Ostrinia furnacalis* (Wang et al. 2001) *Ostrinia nubilalis* (Rosca & Barbulescu 1996) *Spodoptera exigua* (Carpenter et al. 1996) *Spodoptera frugiperda* (Hamm & Carpenter 1997)
Use of F_1 Sterility to Enhance Parasitoids	*Helicoverpa zea* (Proshold et al. 1998) *Plutella xylostella* (Mitchell et al. 1999) *Spodoptera frugiperda* (Proshold et al. 1998)
Field Releases for Suppression	*Cydia molesta* (Genchev 2001) *Cydia pomonella* (Bloem et al. 2001; Chernyi et al. 1996) *Ostrinia furnacalis* (Wang et al. 2001) *Ostrinia nubilalis* (Rosca & Barbulescu 1996) *Plutella xylostella* (Nguyen Thi & Nguyen Thanh 2001; Sutrisno Apu 2001; Yang et al. 2001; Maung 2001)
Population Models	*Cydia pomonella* (Anisimov & Shvedov 1996; Anisimov 1998) *Plutella xylostella* (Carpenter 2000)

mies are underway in Tunisia for suppression of the carob moth, *Ectomyelois ceratoniae*, and on the island of Mauritius for control of the diamondback moth, *Plutella xylostella*. F_1 sterility programs for other lepidopteran pest species also are being considered. Furthermore, the research from the F_1 sterility CRP's contributed to the development of a new Coordinated Research Program on

"Evaluating the Use of Nuclear Techniques for the Colonization and Production of Natural Enemies". This new CRP was initiated in October 1999, with scientific teams from fourteen countries. As one of the research objectives in this new CRP, F_1 sterility is being developed as a tactic to study possible lepidopteran biocontrol agents for invasive noxious weeds (Carpenter et al. 2001).

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