CHAPTER 2.4.

INHERITED STERILITY IN INSECTS

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SUMMARY

The unique genetic phenomena responsible for inherited sterility (IS) in Lepidoptera and some other arthropods, as compared with full sterility, provide advantages for pest control. Lepidopteran females are usually more sensitive to radiation than males of the same species. This allows the radiation dose to be adjusted to suit programme requirements. When partially sterile males mate with wild females, the radiation-induced deleterious effects are inherited by the F_1 generation. As a result, egg hatch is reduced and the resulting offspring are both highly sterile and predominately male. Compared with the high radiation required to achieve full sterility in Lepidoptera, the lower dose of radiation used to induce F_1 sterility increases the quality and competitiveness of the released insects as measured by improved dispersal after release, increased mating ability, and superior sperm competition. F_1 sterile progeny produced in the field enhance the efficacy of released partially sterile males, and improve compatibility with other pest control strategies. In addition, F_1 sterile progeny can be used to increase the production of natural enemies, and to study the potential host and geographical ranges of exotic lepidopteran pests.

1. INTRODUCTION

Lepidopteran species are among the most destructive pests of annual and perennial crops, forests, and stored products throughout the world. Following the successful area-wide integrated pest management (AW-IPM) programme, integrating the sterile insect technique (SIT), against the screwworm fly *Cochliomyia hominivorax* (Coquerel) (Bushland 1971), studies were conducted on the possibility of suppressing lepidopteran pest populations through the release of radiation-sterilized moths. However, because Lepidoptera are radioresistant compared with most other insects (LaChance et al. 1967; Bakri et al., this volume), a dose required to achieve full sterility is so high that it reduces the ability of sterile moths to compete with wild moths. To increase the competitiveness of irradiated Lepidoptera, Proverbs (1962) investigated the effects of substerilizing doses of radiation on the codling moth *Cydia pomonella* (L). He noted that male moths treated with substerilizing doses and then mated to fertile females produced reduced numbers of F_1 progeny, the majority of which were males with very low fertility. This discovery prompted numerous investigations in many lepidopteran pests. North (1975) and LaChance (1985) provide thorough reviews of the early investigations on inherited sterility (IS), and discuss potential advantages of using IS in suppressing pest populations and its possible genetic basis.

IS is also referred to as inherited partial sterility, partial sterility, delayed sterility, semi-sterility and F_1 sterility (Vreysen et al. 2016). Although it is difficult to find a satisfactory definition for IS, LaChance (1985) described several attributes that are common to IS in Lepidoptera: F_1 male and female offspring are more sterile than the irradiated parental (P_1) generation, and more F_1 male progeny than female progeny are produced. Other attributes may include longer developmental time and reduced sperm quality in the F_1 generation. Radiation-induced deleterious effects can be inherited for several generations; however, the majority of the inherited deleterious effects are expressed in the F_1 generation.

2. HISTORICAL OVERVIEW

IS was first reported during studies in the Soviet Union of radiation-induced genetic anomalies in the silkworm *Bombyx mori* (L.) (Astaurov and Frolova 1935). A few years later Ostriakova-Varshaver (1937) reported IS in the greater wax moth *Galleria melonella* (L.). In North America, Proverbs (1962) was the first to describe IS in the codling moth. Within the order Hemiptera, LaChance and Degrugillier (1969) reported IS while conducting genetic studies on the large milkweed bug *Oncopeltus fasciatus* (Dallas), and Delrio and Cavalloro (1975) and Maudlin (1976) documented IS in *Gonocerus acutaeangulatus* (Goeze), a coreid pest of hazelnuts, and in *Rhodnius prolixus* (Stål), a reduviid vector of Chagas' disease, respectively. IS has also been reported in mites of the family Tetranychidae (Henneberry 1964). Although Curtis (1969) and Curtis et al. (1973) found low levels of sterility (5–15%) in the F₁ generation of irradiated tsetse flies (Diptera: Glossinidae), this level of sterility was less than that found in the irradiated parents, and other attributes common to IS in Lepidoptera were not demonstrated in these insects.

The genetic basis for IS has been reviewed and discussed by many authors (Bauer 1967; LaChance 1967, 1974, 1985; LaChance et al. 1970; North and Holt 1970; North 1975; LaChance and Graham 1984; Anisimov et al. 1989; Marec et al. 1999; Tothová and Marec 2001). In this chapter, emphasis will be given to the more recent research findings in the order Lepidoptera. Also the use of genetic sexing, together with IS for the suppression of lepidopteran populations, will be discussed briefly. The advantages of IS as compared with full sterility, the potential for IS to suppress pest populations, and the compatibility of IS with other pest control methods, particularly with biological control, are also discussed. Table 1 provides a comprehensive list of arthropod species where IS has been documented, and includes key references that deal with radiation biology and field studies.

3. GENETICS AND INHERITED STERILITY

No comprehensive review of lepidopteran genetics has been published in the last 45 years. Robinson (1971) provided useful information on formal genetics (including karyology) for many species in this large order. Additional information can be extracted from published research on three economically important species: the silkworm (Tazima 1964; Goldsmith 1995; Fujii et al. 1998; Nagaraju 2000), the Mediterranean flour moth *Ephestia kuehniella* (Zeller) (Caspari and Gottlieb 1975; Leibenguth 1986), and the pink bollworm *Pectinophora gossypiella* (Saunders) (LaChance and Ruud 1980; Bartlett 1989; Bartlett and Del Fosse 1991). Recent advances in the molecular biology and genetics of established and emerging lepidopteran models have been summarized in Goldsmith and Marec (2010).

The lepidopteran genome exhibits a number of peculiarities that distinguishes it from the genomes of other insect orders, except perhaps from that of the closely related order Trichoptera. Chromosomes in Lepidoptera are usually small, numerous, and possess few differentiating features. Most species are reported to have haploid numbers close to 30 ($n = 28\text{--}32$); $n = 31$ appears to be the ancestral number (Ahola et al. 2014). However, karyological studies have identified species

with lower or higher chromosome numbers that are probably the result of chromosome fusion or fission (Suomalainen 1969a; Robinson 1971; reviewed in Marec et al. 2010). Lepidopteran chromosomes are usually spherical and uniform in shape, and consequently not much is known about their morphology, kinetic organization and behaviour during mitotic and meiotic cell division. Lepidopteran chromosomes lack distinct primary constrictions (centromeres) and, as a result, sister chromatids separate by parallel disjunction during mitotic metaphase. Many researchers have concluded that these genomic peculiarities are an indication that lepidopteran chromosomes are holokinetic (Murakami and Imai 1974). However, ultrastructure studies suggest that lepidopteran chromosomes are intermediate between holokinetic and monocentric (Wolf 1996). Nevertheless, a recent functional analysis of the silkworm kinetochore supports the holokinetic structure, although different from the other groups of organisms with holokinetic chromosomes (Mon et al. 2014).

Two other groups of arthropods have shown IS, mites (Acari) and Hemiptera; both possess holokinetic chromosomes and are radioresistant (Brown and Nelson-Rees 1961; Hughes-Schrader and Schrader 1961; LaChance and Degrugillier 1969; Wrensch et al. 1994). Gassner and Klemetson (1974) showed that the kinetochore (centromere) in the large milkweed bug covers more than 70% of the chromosomal surface. Gonzales-Garcia et al. (1996) provided indirect evidence of the holokinetic nature of hemipteran chromosomes while working with *Graphosoma italicum* (Muller) (Pentatomidae). Nonetheless, Wolf (1996) suggests that further investigation is needed to verify the holokinetic nature of hemipteran chromosomes.

The sex chromosomes of Lepidoptera are of the WZ type, in which females are heterogametic (WZ) and males homogametic (ZZ). Lepidopteran species, where sex chromosomes have been identified, show a typical ♀WZ/♂ZZ system, or variants such as Z/ZZ, W₁W₂Z/ZZ or WZ₁Z₂/Z₁Z₁Z₂Z₂ (Suomalainen 1969b; Robinson 1971; Nilsson et al. 1988; Traut and Marec 1997; Rishi et al. 1999; reviewed in Traut et al. 2007 and Marec et al. 2010). Male chromosomes display a normal sequence of meiotic events. In contrast, female chromosomes undergo normal meiosis until they approach the pachytene stage (Fig. 1), when they pair by means of synaptonemal complexes to form bivalents, and synaptonemal complexes become visible (Marec 1996). From this point onwards, female meiosis proceeds without meiotic recombination, and is achiasmate (Traut 1977; Nokkala 1987). The synaptonemal complexes in the female transform into elimination chromatin that later detaches from the bivalents and persists during chromosome segregation in the metaphase plate (Rasmussen 1977). The female W and Z chromosomes, although often non-homologous and of different size, pair completely during meiosis and form a regular bivalent.

Another peculiarity of the lepidopteran genome is the presence of one or more heterochromatic bodies in female somatic cells during interphase. This female specific heterochromatin (also known as W- or sex-chromatin) is derived from the W chromosome. Since sex chromatin is easily identified in interphase nuclei and is especially visible in highly polyploid somatic cells, it can be used as a marker to determine the sex of embryos and larvae and also to identify sex chromosome aberrations in mutagenesis screens (Traut and Marec 1996; Fuková et al. 2009).

Table 1. Arthropod species, including key references of radiation biology and field studies, in which inherited sterility (IS) has been documented

Family, species, and common name	Key references	
	Radiation biology	Field studies
Arachnida – Acari		
Tetranychidae		
<i>Tetranychus urticae</i> Koch twospotted spider mite	Henneberry 1964	
Insecta – Hemiptera		
Coreidae		
<i>Gonocerus acuteangulatus</i> (Goeze) box bug	Delrio and Cavalloro 1975	
Lygaeidae		
<i>Oncopeltus fasciatus</i> (Dallas) large milkweed bug	LaChance and Degrugillier 1969 LaChance et al. 1970	
Reduviidae		
<i>Rhodnius prolixus</i> Stål	Maudlin 1976	
Insecta – Lepidoptera		
Bombycidae		
<i>Bombyx mori</i> (L.) silkworm	Sugai and Mirumachi 1973 Murakami 1976	
Crambidae		
<i>Crociodolomia binotalis</i> (Zeller) cabbage webworm	Sutrisno Apu and Hoedaya 1993	Sutrisno Apu and Hoedaya 1993 Sutrisno Apu 2001
<i>Diatraea saccharalis</i> (F.) sugarcane borer	Walker and Quintana 1968a, b Walker et al. 1971 Sanford 1976; 1977 García and González 1993 González and García 1993	
<i>Ostrinia furnacalis</i> (Guenée) Asian corn borer	Li et al. 1988 Zhang et al. 1993 Wang et al. 2001	Wang et al. 2001
<i>Ostrinia nubilalis</i> (Hübner) European corn borer	Shang and Lo 1980 Nabors and Pless 1981 Rosca and Barbulescu 1990 Barbulescu and Rosca 1993 Rosca and Barbulescu 1993	Barbulescu and Rosca 1993 Rosca and Barbulescu 1993

Table 1. Continued

Family, species, and common name	Key references	
	Radiation biology	Field studies
Gelechiidae		
<i>Pectinophora gossypiella</i> (Saunders) pink bollworm	Cheng and North 1972 Graham et al. 1972 LaChance et al. 1973; 1976 Henneberry and Clayton 1981 Miller et al. 1984 Qureshi et al. 1993a	Bariola et al. 1973 Flint et al. 1974 Qureshi et al. 1993b
<i>Phthorimaea operculella</i> (Zeller) potato tuberworm	Makee and Saour 1997 Makee et al. 2007	
<i>Sitotroga cerealella</i> (Olivier) Angoumois grain moth	Cogburn et al. 1966	
<i>Tuta absoluta</i> (Meyrick) tomato leafminer	Cagnotti et al. 2012 Carabajal Paladino et al. 2016	Cagnotti et al. 2016
Gracillariidae		
<i>Conopomorpha sinensis</i> Bradley litchi stem-end borer	Fu et al. 2016 Zhang et al. 2016	Fu et al. 2016 Zhang et al. 2016
Lymantriidae		
<i>Lymantria dispar</i> (L.) gypsy moth	Mastro et al. 1989 Proshold et al. 1993 Proshold 1995	Maksimovic 1972 Mastro et al. 1989 Mastro 1993 Strom et al. 1996
<i>Teia anartoides</i> Walker painted apple moth	Suckling et al. 2002 Wee et al. 2005	Suckling et al. 2002
Noctuidae		
<i>Agrotis ipsilon</i> (Hufnagel) black cutworm	Elnagar et al. 1984	
<i>Helicoverpa armigera</i> (Hübner) cotton bollworm	Saifutdinov 1989 Ocampo 2001 Sachdev et al. 2014	
<i>Helicoverpa zea</i> (Boddie) corn earworm bollworm tomato fruitworm	Carpenter et al. 1987c Carpenter and Gross 1989 Carpenter 1991; 1992 Carpenter and Wiseman 1992a Hamm and Carpenter 1997	North and Snow 1978 Carpenter et al. 1987a, b; 1989 Carpenter and Gross 1993 Mannion et al. 1994; 1995
<i>Heliothis virescens</i> (F.) tobacco budworm	Proshold and Bartell 1970; 1972a, b; 1973 Guerra and Garcia 1976	North and Snow 1978

Table 1. Continued

Family, species, and common name	Key references	
	Radiation biology	Field studies
Noctuidae		
<i>Spodoptera exigua</i> (Hübner) beet armyworm	Debolt 1973 Carpenter et al. 1996	
<i>Spodoptera frugiperda</i> (J. E. Smith) fall armyworm	Carpenter et al. 1983; 1986; 1997 Carpenter and Young 1991 Arthur et al. 1993 Hamm and Carpenter 1997	Carpenter et al. 1985 Carpenter and Wiseman 1992b
<i>Spodoptera littoralis</i> Boisduval Egyptian cotton leafworm	Wakid and Hayo 1974 Sallam and Ibrahim 1993	Sallam and Ibrahim 1993
<i>Spodoptera litura</i> (F.) Oriental leafworm taro caterpillar	Seth and Sehgal 1993 Sutrisno Apu et al. 1993 Seth and Sharma 2001 Seth et al. 2016a, b	Seth et al. 2016b
<i>Trichoplusia ni</i> (Hübner) cabbage looper	North and Holt 1968; 1969 Ercelik and Holt 1972 Karpenko and North 1973	Toba et al. 1972
Pieridae		
<i>Pieris brassicae</i> (L.) the large white	Bauer 1967	
Plutellidae		
<i>Plutella xylostella</i> (L.) diamondback moth	Omar and Mansor 1993 Sutrisno Apu and Hoedaya 1993 Sutrisno Apu et al. 1993 Nguyen Thi and Nguyen Thanh 2001	Sutrisno Apu and Hoedaya 1993 Okine et al. 1998 Mitchell et al. 1999 Nguyen Thi and Nguyen Thanh 2001 Sutrisno Apu 2001
Pyalidae		
<i>Amyelois transitella</i> (Walker) navel orangeworm	Husseiny and Madsen 1964 Light et al. 2015	
<i>Cactoblastis cactorum</i> (Berg) cactus moth	Carpenter et al. 2001b López-Martínez et al. 2016	Bloem et al. 2003a Hight et al. 2005
<i>Cadra cautella</i> (Walker) almond moth	Ahmed et al. 1971 Gonnen and Calderón 1971 Brower 1980; 1982 Al-Taweel et al. 1990 Makee 1993	

Table 1. Continued

Family, species, and common name	Key references	
	Radiation biology	Field studies
Pyralidae		
<i>Corcyra cephalonica</i> (Stainton) rice moth	Chand and Sehgal 1982	
<i>Eldana saccharina</i> Walker African sugarcane stalk borer	Mudavanhu et al. 2016 Walton and Conlong 2016	
<i>Ephestia kuehniella</i> Zeller Mediterranean flour moth	Riemann 1973 Marec et al. 1999 Tothová and Marec 2001 Ayvaz and Tunçbilek 2006 Ayvaz et al. 2007	
<i>Galleria mellonella</i> (L.) greater wax moth	Nielsen 1971 Nielsen and Lambremont 1976 Nielsen and Brister 1980	
<i>Plodia interpunctella</i> (Hübner) Indian meal moth	Cogburn et al. 1966 Ashrafi et al. 1972 Ashrafi and Roppel 1973 Brower 1976; 1979; 1981 Ayvaz et al. 2008	
Sphingidae		
<i>Manduca sexta</i> (L.) tobacco hornworm	Seth and Reynolds 1993	
Tortricidae		
<i>Cydia pomonella</i> (L.) codling moth	Proverbs 1962 Fossati et al. 1971 Charmillot et al. 1973 Pristavko et al. 1973 White 1975 Anisimov et al. 1989 Bloem et al. 1999a	Charmillot et al. 1973 Charmillot 1977 Proverbs et al. 1978 Bloem et al. 1999b; 2001
<i>Epiphyas postvittana</i> (Walker) light brown apple moth	Soopaya et al. 2011	Woods et al. 2016
<i>Grapholita molesta</i> (Busck) oriental fruit moth	Genchev 2001	Genchev 2001
<i>Lobesia botrana</i> (Denis & Schifferrmüller) European grapevine moth	Steinitz et al. 2015	Saour 2016
<i>Thaumatotibia leucotreta</i> (Meyrick) false codling moth	Schwartz 1978 Bloem et al. 2003b

Figure 1. Examples of pachytene configurations in aberrant chromosomes of Ephesia kuehniella in microspread spermatocytes of F₁ males after the parental male was irradiated with 150 Gy. a: Multiple chain translocation that involves 7 lateral elements, each representing the protein axis of one chromosome, where 1–3 represent structurally normal chromosomes inherited from the untreated female parent; arrows indicate recombination nodules; b: Quadrivalent (Q) typical in reciprocal translocations; c: Ring fragment (arrow) plus a bivalent with one shorter lateral element (idel) that indicates interstitial deletion. All are electron microscope (EM) micrographs stained with phosphotungstic acid. Scale = 2 μ m.

Lepidopteran males undergo two distinct modes of spermatogenesis/meiosis that result in the production of two different types of sperm (Wolf 1994; Friedländer et al. 2005): the larger, nucleate and fertile eupyrene sperm, and the smaller, anucleate and non-fertile apyrene sperm. Apyrene sperm are more abundant and contain less mitochondrial material (Kawamura et al. 1998), while eupyrene sperm are less abundant and typically comprise 10–15% of the total sperm transferred to a female during mating (Gage and Cook 1994; Cook and Wedell 1996). The role of apyrene sperm is not fully understood, although it has been suggested that they aid the transfer of eupyrene sperm to the female (Cook and Wedell 1996), have a nutritive

function (Friedländer 1997), or may be involved in sperm competition. The latter function was studied in *Pieris napi* (L.), where the presence of apyrene sperm was shown to delay female remating (Cook and Wedell 1999).

3.1. Radioresistance in *Lepidoptera*

A high resistance to the effects of ionizing radiation is a characteristic feature of moths and butterflies (LaChance 1985). Cultured lepidopteran cells are 50–100 times more resistant to radiation-induced death than similarly cultured mammalian cells. In contrast dipteran cells are only three to nine times more resistant than mammalian cells (Koval 1996; Chandna et al. 2004). Results of recent studies of a Sf9 cell line, originally derived from *Spodoptera frugiperda*, suggest that several intracellular mechanisms, such as an efficient antioxidant defence and a high activity of histone deacetylases, contribute to the radioresistance of lepidopteran cells (Suman et al. 2015; Sharma et al. 2016). This high radioresistance in *Lepidoptera* also applies to germ cells, and in particular to mature sperm. As a consequence very high doses of radiation are required to fully sterilize lepidopteran males (LaChance and Graham 1984).

LaChance and Graham (1984) and Koval (1996) suggested that possible molecular mechanisms responsible for the high radioresistance in *Lepidoptera* might include an inducible cell recovery system and a DNA repair process. Even though lepidopteran chromosomes are not truly holokinetic, a significant role in their radioresistance can be attributed to their holokinetic “nature” (as first suggested by LaChance et al. 1967) and to the fate of the radiation-induced chromosome fragments during mitotic cell cycles as explained below (Tothová and Marec 2001). Lepidopteran chromosomes possess a localized kinetochore plate to which the spindle microtubules attach during cell division (Gassner and Klemetson 1974; Traut 1986; Wolf and Traut 1991; Wolf et al. 1997). The kinetochore plates are large and cover a significant portion of the chromosome length (Wolf 1996), ensuring that most radiation-induced breaks will not lead to the loss of chromosome fragments as is typical in species with monocentric chromosomes. In species with large kinetochore plates, the fragments may persist for a number of mitotic cell divisions, and can even be transmitted through germ cells to the next generation (Marec and Traut 1993a; Marec et al. 2001). The plates also reduce the risk of lethality caused by the formation of dicentric chromosomes, acentric fragments, and other unstable aberrations (Tothová and Marec 2001) (Fig. 2).

3.2. Radioresistance in *Hemiptera*

A difference in radiosensitivity between males and females has also been documented in several hemipterans including species of economically important leafhoppers (Shipp et al. 1966; Ameresekere and Georgiou 1971) and mealybugs (Brown and Nelson-Rees 1961). However, LaChance and Degrugillier (1969) were the first to document IS in the order Hemiptera when they induced chromosomal fragments and translocations in the large milkweed bug. These authors demonstrated

that the induced fragments were both mitotically and meiotically stable, and could be transmitted through three generations of outcrosses to normal females.

Figure 2. Kinetic structure of lepidopteran chromosomes during mitotic metaphase, and consequences of chromosome breakage; **a**: Holocentric chromosome with two sister chromatids (A₁ and A₂), each with a kinetochore plate (K) covering about 50% of the chromosome surface; spindle microtubules (MTs) are attached to the kinetochore; **b**: Typical monocentric chromosome, where sister chromatids are joined by the centromere (C); the kinetochore is localized on the surface of the centromere.

3.3. Radiation-Induced Sterility in Parental (P₁) Generation

Radiation-induced sterility is generally a consequence of dominant lethal mutations (DLMs) that result in the death of the zygote or the embryo. The chromosomal damage responsible for DLMs is characterized by the formation of anaphase chromosome bridges, chromosome fragments and other abnormalities in the dividing nuclei. In most insects DLMs are expressed during early embryogenesis (LaChance 1967). In Lepidoptera, however, the frequency of DLMs is much lower than in other insects and the majority are expressed very late in embryonic development (LaChance 1974; Berg and LaChance 1976). Furthermore, no chromosomal bridges, indicating the presence of dicentric chromosomes, are evident during embryonic development in Lepidoptera (LaChance and Graham 1984) and Hemiptera studied thus far (LaChance et al. 1970; Maudlin 1976).

For males of four insect species, LaChance and Graham (1984) constructed dose-response curves for the induction of DLMs in mature sperm. The species exhibited a wide range of radiosensitivity, with Hemiptera showing intermediate and Lepidoptera high radioresistance. When analysed mathematically, the dose-response curves approximated an S-shape (LaChance and Graham 1984; Marec et al. 1999). For highly radioresistant Lepidoptera, the curves approximated those expected for 8–16-hit kinetics while in Hemiptera the curve exhibited 4-hit kinetics. These data suggest that multiple chromosome rearrangements must be induced in lepidopteran males to be manifested as DLMs, explaining why lepidopteran males require very high radiation doses (350–500 Gy) to be fully sterilized.

Radiation-induced sterility in lepidopteran males may also have other causes. Anisimov et al. (1989) observed a dose-dependent increase in the number of matings that produced no eggs, or the number of females that laid only unembryonated eggs, following mating with irradiated male codling moths. A significant proportion of unembryonated eggs (that might represent unfertilized eggs and/or eggs with early embryonic mortality) were also observed after treated males were mated to females of *Manduca sexta* (L.) (Seth and Reynolds 1993), *E. kuehniella* (Marec et al. 1999), and *Spodoptera litura* (F.) (Seth and Sharma 2001). Furthermore, Koudelová and Cook (2001) demonstrated with *E. kuehniella* that the volume of sperm transferred during copula decreased, and mating times increased, as the dose increased. Irradiated males of *Tuta absoluta* (Meyrick) produced a significantly higher portion of deformed eupyrene sperm bundles than untreated males (Carabajal Paladino et al. 2016). Taken together, the above data suggest that an important component of male sterility can be due to physiological disruptions during copulation, including the inability to copulate and abnormal sperm transfer.

Lepidopteran females are considerably more radiosensitive than males. In a number of species, a dose of 100 Gy is sufficient to achieve almost full sterility in treated females (Anisimov et al. 1989; Marec and Mirchi 1990; Bloem et al. 1999a) (Fig. 3). It appears that this difference in radiosensitivity between males and females is related to the stage of development of the reproductive cells at the time of irradiation. Lepidoptera are usually irradiated as mature pupae or newly emerged adults. At this stage of development eupyrene spermiogenesis in the male has been completed, and the nuclei in eupyrene sperm are in interphase. In contrast, female meiosis is arrested at metaphase I in the nuclei of mature oocytes and the process does not resume until the eggs have been laid (Traut 1977). As a consequence irradiation of newly emerged females or of mature female pupae may disrupt the normal course of meiosis including chromosome segregation. Finally, various secondary detrimental effects can be expected in oocytes, which have a large amount of cytoplasm (that contains many components required for embryonic development) in comparison with the essentially cytoplasm-free sperm. Almost nothing is known about the radiosensitivity of female Hemiptera, although Delrio and Cavalloro (1975) showed that *G. acuteangulatus* females were fully sterilized at a dose of 50–60 Gy. At this dose males were about 70% sterile.

Figure 3. Percentage egg hatch obtained when codling moth adults were treated with increasing doses of gamma radiation, and either inbred or outcrossed with fertile moths. T = Treated, N = Non-treated. (Figure from Bloem et al. 1999a.)

3.4. Radiation-Induced Sterility in F_1 Generation

Cytogenetic work by Tothová and Marec (2001) showed that various types of translocations (non-reciprocal, reciprocal and multiple) are responsible for the production of genetically unbalanced gametes in F_1 progeny and, as such, represent the main chromosomal mechanism of IS. In addition, they demonstrated that two types of intra-chromosomal aberration, fragmentation, and interstitial deletion increase the frequency of unbalanced gametes; however, their contribution to overall sterility appears to be less significant. The study also revealed that the predicted level of F_1 sterility, based on the observed frequency of aberrations, was much higher than the sterility observed in a previous study (Marec et al. 1999). This suggests that Lepidoptera possess a mechanism that corrects the predicted unbalanced state towards a balanced segregation of chromosomes. The authors suggested that the increased number of chiasmata might facilitate a balanced disjunction of chromosomes from translocation multivalents in F_1 males. The modified synaptonemal complex, which ensures regular disjunction of homologous chromosomes during female meiosis in Lepidoptera (Rasmussen 1977; Marec 1996), might play a similar role in F_1 females (Tothová and Marec 2001).

Several authors have documented the effects of radiation on the incidence of visible chromosomal aberrations in F_1 males using light microscopy (North and Snow 1978; Saifutdinov 1989; Al-Taweel et al. 1990; Carpenter 1991; Carpenter et al. 1997; Carabajal Paladino et al. 2016).

To better understand the principle of inherited sterility, Tothová and Marec (2001) used a modified micro-spreading technique, first employed by Weith and Traut (1980), to study radiation-induced chromosome aberrations in F_1 individuals of *E. kuehniella*. The micro-spread chromosomes were viewed with an electron microscope and several types of aberrations were documented. In F_1 individuals from male parents treated with 100 and 150 Gy, the overall frequency of aberrations

varied between 4.2 and 4.8 per F₁ larva in both sexes. A significant increase in aberrations was found in F₁ males from male parents treated with 200 Gy (6.2 per male). Fragmentation and several types of translocations (non-reciprocal, reciprocal, and multiple) were the most common aberrations, while interstitial deletions and inversions were rare. Multiple translocations forming complicated configurations were found with increasing radiation dose. In males the mean number of chromosomal breaks resulting in aberrations increased linearly with dose, from 8.4 to 16.2 per nucleus. In females this value reached a maximum of 11.2 breaks per nucleus when male parents were treated with a dose of 200 Gy (Fig. 1).

3.5. Sex-Specific Differences in Inherited Sterility

Two consequences of radiation-induced IS are sex-specific and positively correlated with treatment dose. First, the sex ratio of the F₁ generation is skewed toward males (Lepidoptera — Proverbs 1962; Hemiptera — LaChance et al. 1970) and, second, the level of IS in F₁ female progeny is lower than in F₁ males (Lepidoptera — Anisimov et al. 1989; Al-Taweel et al. 1990; Seth and Reynolds 1993; Bloem et al. 1999a).

Marec et al. (1999) suggested that the sex ratio distortion in the F₁ generation in Lepidoptera occurs as a result of recessive lethal mutations induced in the Z sex chromosomes of treated male parents. Since lepidopteran females are heterogametic, all female F₁ progeny will be hemizygous for Z and, as a consequence, any deleterious Z-linked mutations will result in F₁ female mortality. In contrast, the F₁ male progeny will inherit one Z chromosome from the treated father and the other from the mother and, as such, will be heterozygous for any Z-linked mutation.

The induction of F₁ sterility by transmitting complex chromosome translocations to the progeny of treated males was first suggested by North (1967) and North and Holt (1968) for Lepidoptera and by LaChance and Degrugillier (1969) for Hemiptera. Tothová and Marec (2001) suggested three factors that might explain the higher level of sterility found in F₁ male progeny of Lepidoptera:

- The ability of F₁ males to survive even though they inherit a large number of chromosome breaks. The authors found that in F₁ males of *E. kuehniella*, the mean frequency of chromosome breaks was positively correlated with a dose-dependent increase in sterility, whereas a clear correlation was lacking for F₁ females. They suggested that this difference was due to higher mortality in F₁ females that inherit a high number of breaks. Furthermore, at higher treatment doses, there is increased probability that the sex chromosome (Z) will be damaged and, as a consequence, any resulting recessive lethal mutation would kill the F₁ females but not the males. Those F₁ females that survive carry a smaller number of chromosome breaks and, therefore, are more fertile than the F₁ males.
- The occurrence of crossing-over during spermatogenesis. In F₁ males crossing-over during spermatogenesis might increase the number of unbalanced gametes produced, but only if it occurs at the crossover point between an aberrant chromosome (that arose by two or more breaks) and its structurally normal homologue. This situation might occur when inversions and multiple

translocations are formed. However Tothová and Marec (2001) rarely detected inversions in their study on *E. kuehniella*. They concluded that crossing-over contributes to the sterility in F₁ males mostly through the formation of multiple translocations. Since female meiosis is achiasmate during oogenesis, this factor cannot play a role in the sterility level of F₁ females (Rasmussen 1977; Traut 1977; Nokkala 1987; Marec and Traut 1993b).

- A higher impact of radiation-induced deleterious effects on the fertility of F₁ males. Some studies have reported finding a higher number of F₁ male crosses that are fully sterile or that have resulted in the female laying a large number of unembryonated eggs, whereas most F₁ female crosses laid embryonated eggs (Anisimov et al. 1989; Marec et al. 1999). The data suggest that induced genetic changes impaired the fertilizing ability of some F₁ males while the F₁ females were not similarly affected. In addition, Koudelová and Cook (2001) reported great variability in the number of sperm that were transferred by F₁ males of *E. kuehniella*. They found that, on average, the number of eupyrene sperm decreased, whereas the number of apyrene sperm increased, resulting in an abnormally high ratio of apyrene to eupyrene sperm. The ratio fluctuated between 9.5:1 for untreated males and as high as 100:1 for treated males. These results suggest that chromosomal rearrangements in F₁ males may have altered the mechanisms regulating dichotomous spermiogenesis or those underlying copulation and sperm transfer.

3.6. Genetic Sexing in *Lepidoptera*

Genetic sexing has been documented in only two lepidopteran species. Strunnikov (1975) reported that genetic sexing was possible in the silkworm, *B. mori*. About 15 years later Marec (1990, 1991) and Marec and Mirchi (1990) were successful in constructing in *E. kuehniella* a balanced lethal genetic sexing strain, according to the scheme of Strunnikov (1975). This strain, called BL-2, results in males that are trans-heterozygous for two sex-linked recessive lethal mutations, *sl-2* and *sl-15*. When BL-2 males are mated to wild-type females, the F₁ generation consists almost exclusively of male progeny. The F₁ females die during embryogenesis because they inherit one of the lethal mutations from their father, i.e., females are hemizygous for *sl-2* or *sl-15* (Fig. 4).

BL-2 males of *E. kuehniella* could be released directly into nature to introduce lethal mutations into the wild population (Marec et al. 1996), or they could be maintained in the laboratory and used to generate a male-only mutant strain that could be irradiated and released into the environment (Marec et al. 1999). Marec et al. (1999) suggested that the production of male-only colonies through the use of balanced lethal strains would reduce rearing costs and enhance population suppression when used alone or in combination with F₁ sterility. Furthermore, outcrosses of balanced lethal males with wild-type females one generation before irradiation and release would improve the competitiveness of males through positive heterosis. Finally, in addition to the genetic changes induced by treating the males with gamma radiation, the released mutant males would introduce sex-linked recessive lethal mutations into the wild population that would further reduce the

number of F_1 females produced in the field. However, this system relies on sexing two different strains and making directed crosses, and would be impractical in an operational programme.

Figure 4. Genetic sexing system developed in the Mediterranean flour moth; the cross between BL-2 males and wild-type females produces only male progeny. Z and W represent the sex chromosomes; sl-2 and sl-15 are sex-linked recessive mutations. LEL = late embryonic lethality (details in text).

Some significant obstacles still need to be overcome before these types of genetic sexing strain can be used against pest Lepidoptera. For example suitable markers are currently lacking for the construction of similar mutant strains in other economically important species. Also the genetic sexing system requires the mass-rearing of two different colonies, a wild-type strain and a balanced lethal strain, for which sex separation somehow has to be carried out under mass-rearing conditions. Finally, the mutant strain must be routinely checked to prevent the loss of its genetic structure through genetic recombination or colony contamination (Marec 1991; Franz et al., this volume).

Discovery of the sex-determining mechanism in Lepidoptera might facilitate the development of a more convenient and sophisticated sexing system. However, little is known about sex determination in Lepidoptera and, except for the silkworm *B. mori*, the exact locations of the primary sex-determining factors are unknown (Traut and Marec 1996; Traut et al. 2007). In this species, significant progress is being made that will undoubtedly facilitate future research on lepidopteran genetics. Ohbayashi et al. (2001) found a homologue of the *Drosophila doublesex (dsx)* gene in *B. mori* called *Bmdsx*. A sex-specific alternative splicing of the primary *Bmdsx* transcript, along with results of functional studies, strongly suggest that the gene controls sexual differentiation, as does the *Drosophila dsx* gene (Suzuki 2010). In the silkworm, sex determination depends on the presence or absence of the W chromosome, which carries a dominant female-determining factor (*Fem*) (Fujii and Shimada 2007). Recently, Kiuchi et al. (2014) showed that *Fem* is not a protein-coding gene as originally assumed but a W-encoded small RNA named *Fem* piRNA. The *Fem* piRNA controls female-specific splicing of the *Bmdsx* gene by downregulating expression of the Z-linked *Masculinizer (Masc)* gene. It is not known yet if the *Fem* piRNA-*Masc* sex-determining pathway is conserved in other Lepidoptera. Nevertheless, the *dsx* function in sexual differentiation appears to be conserved at the bottom of a sex-determining cascade in many insects including Lepidoptera (Suzuki 2010; Gempe and Beye 2011). Thus, the *dsx* gene may be a good target for the development of genetic sexing strains in pest Lepidoptera.

Advances in genetic technologies, especially in transgenesis, open up new possibilities for genetic sexing in Lepidoptera. Germ-line transformations, with a *piggyBac* transposable element, have been demonstrated — in the pink bollworm by Peloquin et al. (2000) and in the silkworm by Tamura et al. (2000). It has been suggested that genetic sexing strains based on a transgenic approach may be a possible solution to this problem (Marec et al. 2005), where the females would be transgenic but not the sterile males for release. Some progress in developing such strains has been reported in the codling moth (Marec et al. 2007) but this work has not yet been completed. Nevertheless, the feasibility of this approach has been demonstrated recently in the silkworm by the successful insertion of a transgene carrying the EGFP (enhanced green fluorescent protein) reporter into the W chromosome (Ma et al. 2013). Also, a new transgenic conditional lethal genetic sexing system has been developed in the silkworm (Tan et al. 2013) and in two pest species, the diamondback moth and the pink bollworm (Jin et al. 2013). This system is based on the tetracycline-repressible transactivator (tTAV) protein, which is expressed only in females through the alternatively spliced region of the pink bollworm *dsx* gene (*Pgdsx*).

4. ADVANTAGES OF INHERITED STERILITY VERSUS FULL STERILITY

The unique characteristics of IS in Lepidoptera and other arthropods provide some inherent advantages over the use of full sterility in pest control programmes (North 1975). Since lepidopteran females generally are much more radiosensitive than males of the same species, the radiation dose may be adjusted to suit programme requirements, i.e. treated females are completely sterile and males partially sterile.

When these partially sterile males mate with fertile females the radiation-induced deleterious effects are inherited by the F₁ generation. As a result egg hatch is reduced and the resulting (F₁) offspring are both highly sterile and predominately male (Table 2). The lower dose of radiation used to induce F₁ sterility increases the quality and competitiveness of the released insects (North 1975) as measured by improved dispersal after release (Bloem et al. 2001), increased mating ability (Carpenter et al. 1987a), and superior sperm competitiveness (Carpenter et al. 1987a, 1997). In addition, because F₁ sterile progeny are produced in the field, the release of partially sterile males and fully sterile females is more compatible with other pest control mechanisms or strategies (Carpenter 1993; Cagnotti et al. 2016).

Table 2. Typical attributes of male lepidopteran insects (and their progeny) receiving substerilizing doses of radiation

Dose applied to P ₁ (Gy)	1 Egg hatch (%)	2 Larval mortality (%)	3 Sex ratio ♂:♀	4 Egg hatch (%)	
				F ₁ ♂	F ₁ ♀
0	71.8	20.0	1.0:1	82.5	76.8
100	46.1	51.1	2.6:1	10.8	13.9
200	30.8	69.5	5.1:1	0.9	7.5
250	19.1	75.1	7.0:1	0.8	6.1

1. Reduced F₁ egg hatch resulting from P₁ (parental) generation
2. Increased mortality during F₁ development
3. Skewed sex ratio in favor of males in the F₁ generation
4. Reduced F₂ egg hatch resulting from F₁ generation; sterility in F₂ generation higher than in F₁ generation

Data for codling moth (Bloem et al. 1999a)

Knipling (1970) used a mathematical model to explore the application of IS for control of lepidopteran pests (Barclay, this volume). He found that the release of partially sterile insects offered greater suppressive potential than the release of fully sterile insects, and suggested that the partially sterile-to-wild overflooding ratio could be as low as a one-quarter of what is normally required for fully sterile insects. Population models using data collected from several pest species (Walker and Pederson 1969; Brower and Tilton 1975; Carpenter et al. 1987a; Anisimov 1993; Carpenter and Layton 1993; Kean et al. 2011) corroborate Knipling's findings.

5. POTENTIAL FOR INHERITED STERILITY TO SUPPRESS PEST POPULATIONS

Field releases of partially sterile insects have demonstrated the usefulness of IS to control many lepidopteran pests, including the cabbage looper (North and Holt 1969), corn earworm (Carpenter and Gross 1993), gypsy moth (Mastro 1993),

codling moth (Proverbs et al. 1978; Bloem et al. 1999b; Bloem et al. 2001), cactus moth (Hight et al. 2005), and many others (Bloem and Carpenter 2001; Simmons et al., this volume). The effect of F_1 sterility to influence pest populations has been most convincing when irradiated insects have been released in the field throughout the entire growing season. Season-long releases of irradiated (100 Gy) *H. zea* in mountain valleys of North Carolina, USA, delayed and/or reduced seasonal increases of wild *H. zea* males (Carpenter and Gross 1993). The incidence of *H. zea* larvae with chromosomal aberrations indicated that irradiated males were very competitive in mating with wild females, and were successful in producing F_1 progeny, which further reduced the wild population. Release ratios averaged less than 5:1 overall, but reduced the wild population of *H. zea* by more than 70%. In another case, season-long field studies of the codling moth were conducted in apple orchards in Washington State, USA, that compared: (1) twice-weekly releases of partially sterile codling moths treated with either 100 or 250 Gy, and (2) combinations of mating disruption plus the release of partially sterile (100 Gy) codling moths, to control wild populations (Bloem et al. 2001). The results showed that fruit damage was significantly lower in all treatment plots when compared with control plots located outside the treatment areas.

6. COMPATIBILITY OF INHERITED STERILITY WITH OTHER PEST CONTROL METHODS

The success of releasing insects irradiated with substerilizing doses of radiation for the suppression of pest populations is influenced by the ability of released insects and their progeny to survive and interact with the wild population. Field survival rates for F_1 larvae from irradiated parents should be comparable with field survival of wild larvae because many of the deleterious effects induced by radiation are manifested and therefore eliminated during the F_1 egg stage (Carpenter et al. 1985). Any mortality agents such as insecticides, entomopathogens, and natural enemies (parasitoids and predators) could potentially interfere with the effectiveness of F_1 sterility if the agent killed a higher proportion of treated than wild larvae. Likewise host-plant resistance could potentially interfere with the effectiveness of F_1 sterility if the host-plant defenses somehow prevented a higher proportion of treated than wild larvae from establishing and developing on the host plant (Carpenter 1993).

The compatibility of different pest control methods with F_1 sterility has been investigated in both laboratory and field studies. Examples include the use of nuclear polyhedrosis viruses with F_1 sterility for controlling *H. zea* and *Spodoptera frugiperda* (Hamm and Carpenter 1997), host-plant resistance and F_1 sterility in *H. zea* and *S. frugiperda* (Carpenter and Wiseman 1992a, b), F_1 sterility and insecticide resistance in *S. frugiperda* (Carpenter and Young 1991), F_1 sterility and a commercial formulation of *Bacillus thuringiensis* in *P. operculella*, F_1 sterility and synthetic pheromones to reduce wild populations of the codling moth (Bloem et al. 2001), and the use of parasitoids and F_1 sterility (Mannion et al. 1994, 1995; Carpenter et al. 1996; Bloem and Carpenter 2001; Cagnotti et al. 2016; Mangan and Bouyer, this volume). All studies have shown that F_1 sterility is compatible with other pest control methods.

7. POPULATION MODELS COMBINING THE EFFECTS OF F_1 STERILITY WITH OTHER CONTROL METHODS

Knipling (1964), Barclay (1987), and Wong et al. (1992) recognized the potential benefit of combining sterile insects with conventional pest control methods. According to population models (Barclay 1987; Knipling 1992), combining inundative releases of natural enemies and sterile insects should yield additive or synergistic effects. Even though the SIT and natural enemies have different modes of action, the effectiveness of the SIT increases the ratio of natural enemies to adult hosts, and the effectiveness of natural enemies increases the ratio of sterile to fertile insects. Therefore, greater suppression could be expected if parasitoid releases were combined with the F_1 sterility technique (Carpenter 1993). Not only is F_1 sterility theoretically more effective than full sterility in reducing population increase (Carpenter et al. 1987a), but F_1 sterility results in the production of sterile F_1 eggs and larvae that provide an increased number of hosts for parasitoids. As a result, the number of parasitoids produced should increase even if the rate of parasitism remained the same (host-density independent), and whether or not additional parasitoids are released. Although population models (that independently consider augmentative releases of parasitoids (Knipling 1992) and F_1 sterility (Carpenter et al. 1987a)) suggest that both methods are highly efficacious, integrating lepidopteran F_1 sterility and augmentative biological control results in synergistic effects (Carpenter 1993). Therefore, the greatest impact of F_1 sterility and augmentative parasitoid releases as area-wide methods against lepidopteran pests can be realized only when the two methods are integrated (Barclay, this volume).

Population models also provide insight into how different control strategies could be combined for greatest efficiency. Although the effectiveness of F_1 sterility continues to increase as the ratio of irradiated to non-irradiated insects increases, the efficiency per released moth declines. A similar loss of efficiency occurs in parasitoid releases (Carpenter 1993). According to these models the economic benefit of combining F_1 sterility and parasitoid augmentation would be greatest when the ratios of irradiated to non-irradiated, and parasitoid to host, are low (i.e. equal to or less than 10:1). The model presented in Fig. 5 demonstrates that population suppression is increased when F_1 sterility and parasitoid releases are combined, and that the percentage reduction in population growth is greater when parasitized hosts produce adult parasitoids than when no parasitoids are produced (Carpenter 2000).

8. INHERITED STERILITY IN COMBINATION WITH BIOLOGICAL CONTROL

Fully successful integration of F_1 sterility and parasitoid augmentation into a management approach can occur only if parasitoids do not negatively impact irradiated insects and their progeny more than that of the wild population, and if F_1 sterility does not negatively impact the efficacy and reproduction of parasitoids. Knowledge of any negative impact of F_1 sterility on parasitoids would be important before implementing an AW-IPM programme using F_1 sterility. For example, if

parasitoids that attack the F₁ sterile progeny are unable to develop normally, and most of the hosts present are F₁ sterile progeny, then there could be a negative impact on subsequent parasitoid populations. Conversely, if parasitoids develop normally on F₁ eggs, larvae, and pupae, then the greater number of hosts available would allow for an increase in the parasitoid population. Since many hosts of the F₁ generation would experience genetically-induced mortality before they reached the adult stage, any parasitoids able to develop on these hosts would result in a positive and synergistic increase in the efficacy of an AW-IPM programme (Carpenter 2000).

Figure 5. Comparison of the projected reduction in normal population growth when only parasitoids [parasites] are released (Knippling 1992), when only irradiated (100 Gy) male moths are released (Carpenter et al. 1987c), and when releases are equally divided between parasitoids and irradiated male moths.

Field, greenhouse and laboratory studies compared the acceptability and suitability of progeny from irradiated (100 Gy) and untreated *Spodoptera exigua* males as hosts for the braconid larval parasitoid *Cotesia marginiventris* (Cresson) (Carpenter et al. 1996), and progeny from irradiated (100 Gy) and untreated *H. zea* males as hosts for the tachinid *Archytas marmoratus* (Townsend) (Mannion et al. 1994, 1995). Results from these studies demonstrated that progeny of irradiated males and untreated females were acceptable and equally suitable hosts for parasitoid development. Female parasitoids showed no oviposition preference for progeny from females paired with either irradiated or untreated males. Other studies on different lepidopteran pests also have reported compatibility between the two control methods (Bloem and Carpenter 2001).

There are many different scenarios in which F₁ sterility could be integrated with natural enemies to suppress pest populations (Carpenter 1993; Hendrichs et al. 2009) (Box 1). The release of partially sterile males and fully sterile females would produce large numbers of F₁ eggs and larvae that could be field-reared on early-season host plants or crop plants that tolerate some larval feeding damage, e.g.

whorl-stage corn. Natural enemies (native and/or released) could use the F₁ eggs, larvae and pupae as hosts and thereby substantially increase the natural enemy population for the next generation of the pest insect (Proshold et al. 1998). Also surviving sterile F₁ progeny would produce sterile adults that would negatively impact the next generation of the pest insect. If the economic injury level of cultivated host plants indicated that the additional sterile F₁ larvae were undesirable, then the dose of radiation could be increased to a level that would reduce or eliminate the number of progeny from irradiated females, or releases could be limited to irradiated males.

Box 1. Opportunities for Combining Inherited Sterility with Biological Control

For pest suppression:

- Simultaneous or sequential inundative releases of irradiated insects and natural enemies
- Irradiated insects and their sterile progeny serve as host/prey for wild natural enemies.

For research:

- Elucidation of the potential host range of exotic pests
- Prediction of the potential geographic range of exotic pests
- Delineation of the potential impact of native natural enemies on invading pests.

Although the compatibility of F₁ sterility with the application of synthetic organic insecticides has been demonstrated (Carpenter and Young 1991), parasitoids and/or predators generally are not compatible with these products. When insecticides are required to reduce pest infestations, insect growth regulators or other formulations that are compatible with natural enemies should be considered. Another management option would be to establish host plants for the pest in insecticide-free areas adjacent to insecticide-treated crops. Host plants could be artificially infested with pest larvae to provide natural enemies (native and/or released) with an adequate supply of hosts. If the pest larvae used in the artificial infestations (nursery crops) were sterile, i.e. the progeny of irradiated parents, then non-parasitized larvae would not contribute to the increase of the wild population but would produce sterile adults that would negatively impact the next generation of the pest insect (Okine et al. 1998; Carpenter 2000).

In addition to using F₁ sterility as a direct pest control method, there are opportunities to use F₁ sterility to facilitate the development of other pest suppression methods. For example the F₁ sterile progeny (eggs, larvae and pupae) of a pest may be used as hosts/prey for natural enemies that are shipped commercially, especially in quarantine-sensitive shipments (Hendrichs et al. 2009). The use of sterile insects in commercial shipments would ameliorate concerns regarding the reproductive viability of non-parasitized and non-consumed pests upon arrival at the shipment destination. Also the use of F₁ sterile progeny as hosts for parasitoids would eliminate the need to wait for non-parasitized pests (either eggs or pupae) to emerge before shipment of the parasitized pest (Greany and Carpenter 2000; Hendrichs et al. 2009).

9. ADDITIONAL APPLICATIONS OF F₁ STERILITY FOR RESEARCH AND MANAGEMENT

Greany and Carpenter (2000) reported that F₁ sterility could provide a new risk management tool for assessing the safety of exotic lepidopterans being considered as biological control agents against invasive weeds (Moeri et al. 2009; Tate et al. 2009) (Box 1). Production of F₁ sterile progeny permits developmental and behavioral observations to be made under actual field conditions without concern that a breeding population would be established (Carpenter et al. 2001a). This facilitates field observations on oviposition behaviours and host associations, larval feeding preferences, and larval development and survival on both target and non-target plant species. Also, the impact that native natural enemies might have on exotic candidate species being considered as biological control agents for invasive weeds, and the ability of these candidate species to survive and overwinter under various climatic conditions could be studied in the field through this innovative application of F₁ sterility.

F₁ sterility could be used to conduct research on exotic pests that are expanding their geographical range. Strom et al. (1996) suggested that gypsy moth host preferences, or the quality of potential hosts outside the generally infested area, could be investigated using releases of F₁ sterile larvae of *L. dispar*. In addition to host range studies, Carpenter et al. (2001a) suggested that F₁ sterility could be used to predict the potential geographic range and to evaluate the potential impact of native natural enemies on the rate of spread of exotic lepidopteran pests.

10. CHALLENGES AND OPPORTUNITIES

Challenges are inherent in all pest management methods, and Whitten and Mahon (this volume) discuss constraints and misconceptions unique to the SIT. In addition to those in common with the SIT, the major challenge to the use of IS is the perception that sterile F₁ larvae cause economic damage to crops, especially high-value crops such as fruit. Consequently, low doses of radiation, which would certainly result in more competitive insects, are often avoided. For example, Proverbs et al. (1978) found that codling moths treated with 250 Gy were more competitive in the field, and provided better control, than did fully sterile moths (400 Gy). Nevertheless, in spite of these findings, Proverbs et al. (1982) continued to be concerned that F₁ larvae would cause economic damage, and used 350 Gy to irradiate moths released in a pilot study conducted in British Columbia, Canada, from 1976–1978. Also, in the current codling moth programme in British Columbia, Canada, which began field operations in 1994, moths treated with 350 Gy are released, even though doses as low as 100 Gy have been suggested (Anisimov 1993; Bloem et al. 1999a, 1999b). It was found in field studies that season-long releases of moths treated with 100 Gy did not cause fruit injury (Fig. 6), and moths receiving 100 Gy were more competitive than those receiving 250 Gy (Bloem et al. 2001). These studies indicate that fears of increased fruit (or plant) injury resulting from F₁ larvae are ill founded, especially when the radiation dose causes partial sterility in males and full sterility in females. Therefore, the production of sterile F₁ larvae

should be seen not as a problem but rather an opportunity to enhance the production of natural enemies and to produce more competitive sterile moths in the field.

Figure 6. Percentage fruit damage at harvest caused by the codling moth in apple orchards in Washington State, USA. One series of three plots received season-long releases of partially sterile codling moths treated with 100 Gy (female moths were 100% sterile, and males 50% sterile). A second group of plots received 250-Gy-treated moths (females 100% sterile, and males 75% sterile). The control areas were treated with six applications of azinphosmethyl insecticide. At the end of the fruiting season, 2500 fruit per treatment were sampled (Bloem et al. 2001).

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