CHAPTER 3.4.

STERILIZING INSECTS WITH IONIZING RADIATION

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SUMMARY

Exposure to ionizing radiation is currently the method of choice for rendering insects reproductively sterile for area-wide integrated pest management (AW-IPM) programmes that integrate the sterile insect technique (SIT). Gamma radiation from isotopic sources (mainly cobalt-60 or decreasingly caesium-137) is commonly used, but high-energy electrons and X-rays are other practical options. Recently, the development of self-contained low-energy X-ray irradiators for insect sterilization is being encouraged because they only require access to electricity and cooling water, and avoid the complex and costly shipment of radioactive sources across international borders. Insect irradiation is safe and reliable when established safety and quality-assurance guidelines are followed. The key processing parameter is absorbed dose, which must be tightly controlled to ensure that treated insects are sufficiently sterile in their reproductive cells and yet able to compete for mates with wild insects. To that end, accurate dosimetry (measurement of absorbed dose) is critical. Data from more than 5300 studies on irradiation since the 1950s, covering more than 360 arthropod species (IDIDAS database), indicate that the dose needed for sterilization of arthropods varies from less than 5 Gy for the acridid *Schistocerca gregaria* (Forskål) to 400 Gy or more for some lyonetiid, noctuid, and pyralid moths. Factors such as oxygen level, insect age and stage during irradiation, and many others, influence both the absorbed dose required for sterilization and the viability of irradiated insects. Consideration of these factors in the design of irradiation protocols can help to find a balance between the sterility and competitiveness of insects produced for programmes that release sterile insects. Some programmes prefer to apply “precautionary” radiation doses to increase the security margin of sterilization, but this overdosing often lowers competitiveness to the point where the overall induced sterility in the wild population is reduced significantly.

1. INTRODUCTION

The potential of ionizing radiation to interact with materials has numerous applications in industry, medicine, and agriculture (Arthur et al. 2015; IAEA 2018). Ionizing radiation breaks down molecules, causing various effects in irradiated material. Radiation can cause polymerization of plastics, and can kill pathogens and other micro-organisms, leading to applications in food processing and the sterilization of health-care products. In organisms, which are composed of differentiated and undifferentiated cells, mitotically active cells, such as stem and germ cells, are the most radiation-sensitive cells. In the case of the sterile insect technique (SIT) and related biocontrol applications, as well as post-harvest quarantine treatments (Heather and Hallman 2008; Bloem et al. 2009), radiation can make an insect reproductively sterile by damaging the chromosomes of gonial cells. Specifically it causes germ-cell chromosome fragmentation (dominant lethal mutations, translocations, and other chromosomal aberrations), leading to the production of imbalanced gametes and subsequently the inhibition of mitosis and death of fertilized eggs or embryos (Klassen and Vreysen, this volume; Robinson, this volume). In adult insects, midgut stem cells, which undergo continuing mitotic divisions (such as in the cotton boll weevil *Anthonomus grandis grandis* Boheman), are particularly sensitive to ionizing irradiation, and the irradiation of certain species may cause a significant reduction in lifespan and increased mortality (Riemann and Flint 1967). Nevertheless, the successful sterilization of other radiation-sensitive insect species, without a reduction in their lifespan, may indicate that the effect on cell replacement in the midgut could be mitigated (Sakurai et al. 2000). Differentiated somatic cells are generally less sensitive to radiation than are stem cells. Thus a lethal effect requires a higher radiation dose than a reproductive sterilization effect. The impact of radiation on somatic cells is expressed as the development of abnormalities, a reduction in lifespan, flight ability, mating propensity, and nutrition, and finally insect death.

Radiation sterilization of insects is a relatively straightforward process, with reliable quality control procedures. The key parameter is the radiation absorbed dose which is expressed in Système International d'Unités (SI) units as gray (Gy) (1 Gy = 100 rad), where 1 Gy is equivalent to 1 joule (J) of absorbed energy in 1 kg of a specified material (1 Gy = 1 J/kg). As long as the correct dose is delivered at the appropriate stage of development, efficacy of the irradiation process is guaranteed.

Other advantages of using radiation to sterilize insects include: (1) temperature rise during the process is insignificant, (2) sterile insects can be released immediately after processing, (3) irradiation, unlike chemosterilants, does not add residues that could be harmful to human health or the environment, and (4) radiation can pass through packaging material, allowing insects (or commodities in the case of post-harvest treatments) to be irradiated after having been packaged.

In the 1950s and 1960s, numerous mutagenic chemicals were tested as alternatives to radiation to induce sterility in insects (Knipling 1979; Klassen and Vreysen, this volume; Lance and McInnis, this volume). Chemosterilants were added to rearing diets, applied topically to insects, or even deployed in attractant-baited devices in the field. The efficacies of irradiating and chemosterilizing insects for population control were, in general, similar (Guerra et al. 1972; Flint et al. 1975; Moursy et al. 1988). However, today, chemosterilants are not used for sterilizing mass-reared insects. Most

chemosterilants that were investigated in early studies are carcinogenic, mutagenic, and/or teratogenic, leading to environmental and human-health issues such as the integrity of ecological food chains, waste disposal, e.g. spent insect diet, and worker safety (Hayes 1968; Bracken and Dondale 1972; Bartlett and Staten 1996). More recently, a group of less broadly toxic compounds (insect growth regulators) has been studied as chemosterilants, but primarily as alternative insecticides, or in attractive autodissemination devices, rather than for use in SIT projects, e.g. Casaña-Giner et al. 1999; Moya et al. 2010; Bouyer and Lefrancois 2014). Insect resistance to chemosterilants is an additional concern (Klassen and Matsumura 1966).

Sterile insects are also being produced that are transgenic and contain conditionally expressed dominant lethals (Thomas et al. 2000; Harris et al. 2011; Häcker et al., this volume). However, at this time, exposure to ionizing radiation is still the principal method of inducing sterility for area-wide integrated pest management (AW-IPM) programmes that release sterile insects.

2. RADIATION SOURCES

The suitability of a radiation type for the SIT depends on properties, such as relative biological effectiveness (RBE), penetrability, availability, safety, and cost. The RBE of radiation is defined as the ratio dose X/dose R, i.e. the dose of 200–250 kV X-rays required to produce a specific biological effect to the dose of radiation (R) required to produce the same effect. The RBE of radiation for the induction of chromosome aberrations depends on its linear energy transfer (LET — the energy imparted to a medium by a charged particle of a specified energy, per unit distance). Radiation with a higher LET is more effective in inducing sterility, and most likely would yield insects that are more competitive (North 1975). However, a higher LET also means that penetration is limited. For example, alpha particles have a high value of LET, but can penetrate only a fraction of a millimetre into a container of insects, which makes them unsuitable to sterilize insects for release in AW-IPM programmes. Neutrons are more effective than gamma radiation or X-rays in sterilizing insects (Hooper 1971; North 1975; Offori and Czock 1975). However, neutrons can induce radioactivity in irradiated materials, which, along with the immobility of nuclear reactors (the usual source of neutrons), makes their use impractical for most programmes.

Considering this, the types of radiation that can be used practically in programmes that release sterile insects include gamma radiation, high-energy electrons, and X-rays (Bushland and Hopkins 1951, 1953; Baumhover et al. 1955; Lindquist 1955). All have similar effects on materials, and in particular on insects (since they have a similar RBE). For certain insect life stages and radiation doses, several studies found no significant difference between electrons and gamma radiation in their lethal effects (Hooper 1971; Adem et al. 1978; Watters 1979; Dohino et al. 1994).

To maintain the fitness of irradiated insects, and for the safety of workers, the induction of radioactivity in irradiated materials, such as canisters and insects, must be avoided. This is achieved by ensuring that the particle energy used for the SIT is less than 5 million electron volts (MeV) for photons (gamma radiation or X-rays), and below 10 MeV for electrons (Elias and Cohen 1977; Codex Alimentarius 1983; FAO/IAEA/WHO 1999; IAEA 2002a). Thus, gamma radiation from cobalt-60 (Co-

60) (photon energies are 1.17 and 1.33 MeV) and caesium-137 (Cs-137) (0.66 MeV), electrons generated by accelerators with energy less than 10 MeV, and X-rays generated from electron beams with energy below 5 MeV, are acceptable for sterilizing insects.

2.1. Radioisotopes

Currently, the most commonly used radiation for the SIT is gamma radiation from the radioisotopes Co-60 and Cs-137. These isotopes have long half-lives, and the energy of their gamma radiation is relatively high (Table 1). To provide the same throughput, caesium sources, because of the lower photon energy, require about four times more activity than cobalt sources. Cobalt-60 is produced by placing small cylinders of natural cobalt (which is 100% Co-59) into a nuclear reactor, where the Co-59 atoms absorb neutrons and are converted into Co-60. These cylinders are removed from the reactor after 1 or 2 years, and are further encapsulated in corrosion-resistant stainless steel cylinders to produce source "pencils". Caesium-137 is produced from the fission of uranium and plutonium, and must be chemically separated from other fission products and actinides present in used nuclear fuel. The use of caesium for radiation purposes is declining because this process is very elaborate, and also in view of the danger its water solubility represents in terms of potential use for terrorism.

Table 1. Comparison of properties of Co-60 and Cs-137

Property	Co-60	Cs-137
Production mode	Neutron absorption in nuclear reactors	Chemical separation from spent nuclear fuel, e.g. uranium
Half-life	5.271 years	30.07 years
Photon energy	1.17 and 1.33 MeV (in equal proportions)	0.66 MeV
50% dose-decrease (depth in water)	23 cm	21 cm

2.2. Electron Beam

Even though high-energy (5–10 MeV) electrons can be used to sterilize insects, because of the cost and size of an electron beam facility it is normally not a suitable option. The exception would be if there is such a facility in the vicinity that is being used for other purposes. In such cases, the facility could be leased for a limited time period and at an affordable cost. An example is the Mediterranean fruit fly *Ceratitis capitata* (Wiedemann) facility in Valencia, Spain. Such electrons are generated by an electron accelerator, which does not involve any radioactive materials. Electrons are

introduced into an accelerating structure from an injector, where they are accelerated to the designed high energy that can be derived from a variety of sources depending on the type of accelerator. An electron accelerator yields a narrow and intense electron beam, and thus the dose rate can be up to 1000 times greater than from a gamma irradiator. However, gamma radiation from Co-60 or Cs-137 penetrates irradiated materials more deeply than electrons. For example, for Co-60 gamma rays, dose decreases only to half at a depth of about 23 cm in water, but for 10-MeV electrons the useful depth is only about 4 cm.

2.3. *X-Rays*

When a beam of electrons strikes material with a high atomic number, e.g. tungsten, X-rays are generated. X-rays, like gamma radiation, are electromagnetic radiation. Radiation generated in this manner (by the rapid deceleration of a charged particle) is also known as “Bremsstrahlung”. While gamma radiation from radioisotopes has discrete energies, Bremsstrahlung has a broad energy spectrum with a maximum equal to the energy of the incident electrons. The penetration of 5-MeV X-rays is similar to that for Co-60 gamma radiation and therefore higher than that for electrons.

3. RADIATION TECHNOLOGY AND STERILIZATION PROCESS

3.1. *Irradiation Facilities*

The design of an irradiation facility affects the dose distribution and the attainable dose range. It may be designed either for a specific application (or product) or for multiple applications, depending on local considerations and user requirements. The basic components of an irradiation facility include:

- Radiation source (radioisotopic gamma source, X-ray tube or electron accelerator) and the associated control systems,
- System for transporting the product, e.g. insects, or in some cases the source, to and from the position at which irradiation occurs,
- Shielding to protect workers and the surrounding environment from radiation.

The irradiation facility should also include a dosimetry laboratory, and a product-handling system with areas designated for receiving and for segregated pre- and post-irradiation storage.

3.1.1. *Gamma Irradiators*

The radiation source consists typically of several source pencils of either cobalt or caesium. The dose rate is determined by the current activity (strength) of the source, and the operator controls the absorbed dose delivered to the insects by adjusting the time that they are exposed to radiation (an exception — in some large-scale irradiators, several dose rates can be obtained by raising different subsets of the source pencils into the irradiation room). The only variation in the source output is the known reduction in activity caused by radioactive decay, which can have a significant impact on the programme (financial as well as scheduling irradiation operations) if

not taken into account. The activity of a cobalt source, for example, decreases by about 12% annually. The irradiator operator compensates for this loss of activity by incrementally increasing irradiation time (approximately 1% each month) to maintain the same dose given to the insects. Since irradiation times eventually become impractically long, sources need to be replenished at regular intervals, depending on the initial activity of the source and the operational requirements.

Typically there are two types of gamma irradiators used in programmes that release sterile insects — self-contained dry-storage irradiators, and large-scale panoramic irradiators.

Self-Contained Dry-Storage Irradiators. At present, most sterilization of insects is accomplished using gamma radiation from self-contained irradiators (Fig. 1). These devices house the radiation source within a protective shield of lead, or other appropriate high-atomic number material, and they usually have a mechanism to rotate or lower the canister of insects from the loading position to the irradiation position. These canisters, which are reusable and generally made of steel, aluminium, or plastic, hold packaging containers with insects during irradiation. To irradiate, a canister is placed in the irradiation chamber while it is in the loading (shielded) position and, depending on the current dose rate of the irradiator, the timer is set to deliver the pre-selected dose. On the push of a button, the chamber is automatically moved to the irradiation position. In most self-contained irradiators, the irradiation position is in the centre of an annular (circular) array of long parallel pencils that contain the encapsulated radionuclide. With this design, the dose is relatively uniform within the irradiation chamber (section 3.3.2.). In an alternative configuration, the radionuclide is contained in a single rod. In this case, the canister with insects is rotated on a turntable within the irradiation chamber to achieve an acceptably uniform dose. The axis of rotation is parallel to the source rod, which is usually vertical. The canister stays in the irradiation position for the set time interval, and then automatically moves to the unloading (shielded) position at the end of the treatment. Self-contained dry-storage irradiators provide a high dose rate but a small irradiation volume (1 to 4 litres), and are suitable for research as well as small-scale programmes that apply the SIT.

Large-Scale Panoramic Irradiators. For large-volume irradiation, panoramic irradiators are more suitable. The source consists of either several Co-60 rods (pencils) arranged in a plane or a single rod that can be raised/lowered into a large irradiation room. When retracted from this room, the source is shielded either by water (wet storage), or by lead or other appropriate high-atomic-number material (dry storage). Since isotopic sources emit gamma radiation isotropically (in all directions), they may be surrounded by canisters of insects to increase the energy utilization efficiency, and several canisters can be irradiated simultaneously.

Figure 1. In preparation for irradiation, a canister with insects is placed in the irradiation chamber (while it is in the shielded position) of a self-contained gamma irradiator. Depending on the dose rate of the day, the timer on the control panel (lower right) is set to give the desired dose.

Many large-scale irradiators run in a continuous-operation mode, in which canisters of insects are carried on a conveyor around a central source. The canisters may pass by the source several times to increase dose uniformity in the canisters as well as energy utilization. The speed of the conveyor is selected so that the insects receive the intended dose. The source is moved to the storage position only when the irradiator is not in use. An alternate method is batch operation, where several canisters of insects are placed in the irradiation room while the source is in its storage position. The source is then moved into the irradiation room for the length of time required to achieve the desired absorbed dose. To improve dose uniformity, each canister may be rotated on its own axis during irradiation using turntables.

3.1.2. Self-Contained Low-Energy X-Ray Irradiators

Recently, self-contained low-energy X-ray irradiators (Fig. 2) suitable for SIT applications have become commercially available (Wagner et al. 2009; Mastrangelo et al. 2010; Mehta and Parker 2011). The maximum X-ray energy for these irradiators is about 160 keV, and thus shielding requirements are less than for a typical self-contained gamma irradiator. These irradiators utilize X-ray tubes that consist of an electron source (generally a heated wire, a filament which emits electrons), an

electrostatic field to accelerate these electrons, and a converter to generate X-rays. In the currently available irradiators, the converter is present throughout the curved surface of the tube, and hence the X-rays are emitted in all directions. One method for irradiating insects is to operate the irradiator in a batch mode where several canisters of insects are placed around and parallel to the X-ray tube, and revolve around the tube during irradiation while maintaining their orientation (much like chairs on a Ferris wheel), achieving acceptable dose uniformity. An alternate method is to continuously pass trays with insects between two X-ray tubes, providing irradiation from two sides.

Figure 2. A typical X-ray irradiator (self-shielded X-ray irradiator) consisting of two units: the exposure chamber (in the foreground) houses the X-ray tube and the canisters with insects, and the second unit (in the background) houses the water tank and cooling fans. (Photo from A. G. Parker, reproduced with permission.)

3.1.3. Electron Accelerators

Accelerator-generated radiation has two modes, electrons and X-rays produced from these electrons (Fig. 3). The two principal electron-beam characteristics are beam (electron) energy in MeV, and the average current in milliamperes (mA). These accelerators generally produce electrons of energy up to 10 MeV, and hence the irradiators need to be housed in heavily shielded rooms (unlike self-shielded irradiators). The beam energy determines the penetration of electrons in a material (thus dictating the useful size of the canister for irradiation), and the average beam current affects absorbed-dose rate (thus determining throughput, e.g. the number of canisters treated per hour). Unlike gamma radiation, radiation beams for such

irradiators are rather focused (for both modes), and typically conveyors are used to move canisters of insects continuously through the beam. Also, the electron beam (and also X-ray beam) is scanned to cover the length and width of the insect container, generally a tray. Since X-rays penetrate deeper than the electrons, from which they are generated, larger canisters of insects can be used when using the X-ray mode. To improve dose uniformity, each canister may be rotated on its own axis during irradiation using turntables.

Figure 3. Electron beam irradiation facility equipped with an electron accelerator and electron-to-X radiation converter. (Photo from Ion Beam Applications (iba), reproduced with permission.)

3.1.4. Selection of Irradiator

Since gamma radiation, X-rays and electrons have similar sterilizing effects, the choice of source for SIT irradiation is based on other considerations, such as penetration, cost, product throughput (Mehta 2009; DIR-SIT 2018), as well as expertise available at the site, and environmental, safety and security factors. The shallow penetration of electrons restricts the size of the canister used for irradiation. In addition, gamma irradiators, as well as the new self-contained X-ray irradiators, are usually simpler to operate and less expensive than large electron accelerators, at least within the range of the power required for SIT applications. However, X-rays and electron accelerators may have more public acceptance because they produce no radiation when switched off, and there are no transportation or radioactive waste issues (Cavalloro and Delrio 1974; Piedade-Guerreiro and Gomes da Silva 1983; Cleland and Pageau 1985; Smittle 1993; EBFRT 2004; FDACS 2018).

The power emitted by a gamma-ray source containing 100 kCi of Co-60 is roughly equivalent to that of a 1.5 kW electron accelerator. The power capacity of currently available commercial accelerators with 5–10 MeV electrons is usually much greater than this, making them unsuitable for dedicated SIT use. X-ray irradiators have the advantages of both gamma irradiators (high penetrability) and accelerators (no radiation when switched off). Based on all of these factors, almost all current insect sterilization programmes have traditionally used gamma irradiators (Table 2).

Table 2. Examples of insect mass-rearing facilities, and the types of irradiators used for reproductive sterilization (more extensive list found in DIR-SIT 2018)

Location of facility	Insect reared	Dose (Gy) ¹	Initial activity (kCi)	Irradiator model (MANUFACTURER)	Source
Argentina	<i>Ceratitis capitata</i> ⁴	110	20	IMCO-20 ²	Co-60
Brazil	<i>Ceratitis capitata</i>	115		RS2400 (RadSource Technologies) 125 keV, 18 mA	X-ray
	<i>Aedes aegypti</i> ⁵	65			
Burkina Faso	<i>Glossina palpalis gambiensis</i> ⁶	110	12	GAAA (Groupement Atomique Alsacienne Atlantique)	Cs-137
Canada	<i>Cydia pomonella</i> ⁷	150	24	Gammacell [®] 220 ² (NORDION)	Co-60
Chile	<i>Ceratitis capitata</i>	120	16	Gammacell [®] 220 ² (NORDION)	Co-60
China	<i>Aedes albopictus</i> ⁸	50		Wolbaki (Tongda Dandong, China) 160 keV, 16 mA	X-ray
Costa Rica	<i>Ceratitis capitata</i>	150		RS2400 (RadSource Technologies) 150 keV, 45 mA	X-ray
France (Reunion)	<i>Aedes albopictus</i>	35		BloodXrad (Cegelec Actemium NDT-PES) 160 keV	X-ray
Guatemala	<i>Ceratitis capitata</i> <i>Anastrepha ludens</i> ⁹	100–145	11	Gammacell [®] 220 E ² (2 units) (NORDION)	Co-60
		80	12	Gammacell [®] 220 R ² (J. L. SHEPHERD)	Co-60
			80	Process Irradiator 484C-P ² (J. L. SHEPHERD)	Co-60
			42	Husman 521A ² (ISOMEDIX)	Cs-137
			46	Husman 521 ² (ISOMEDIX)	Cs-137

Table 2. Continued

Location of facility	Insect reared	Dose (Gy) ¹	Initial activity (kCi)	Irradiator model (MANUFACTURER)	Source
Israel	<i>Ceratitis capitata</i>	100	12	Gammacell® 220 E ²	Co-60
	<i>Bactrocera oleae</i> ¹⁰	100			
Japan	<i>Cylas formicarius</i> ¹¹	200	97.8	C-188 ³ (NORDION)	Co-60
	<i>Euscepes postfasciatus</i> ¹²	150			
Mexico	<i>Anastrepha ludens</i>	80	59.9	GB-127 ³	Co-60
	<i>Anastrepha obliqua</i> ¹³	80	59.9	GB-127 ³	Co-60
	<i>Ceratitis capitata</i>	100	27.9	JS-7400 ³ (2 units) (NORDION)	Co-60
	<i>Cochliomyia hominivorax</i> ¹⁴	55	19.5	Model 7810-150 ² (J. L. SHEPHERD & ASSOCIATES)	Co-60
Philippines	<i>Bactrocera dorsalis</i> ¹⁵	64–104	30	GB 651 PT ³ (NORDION)	Co-60
South Africa	<i>Ceratitis capitata</i>	90	10	(LOCAL MANUFACTURER) ³	Co-60
	<i>Thaumatotibia leucotreta</i> ¹⁶	150	20	Point Source Panoramic ³	Co-60
Spain	<i>Ceratitis capitata</i>	95		Rhodotron TT200 (Ion Beam Applications) 10 MeV, 8 mA	E-Beam
Thailand	<i>Bactrocera dorsalis</i>	90	24	Gammacell® 220 ² (NORDION)	Co-60
	<i>Bactrocera correcta</i> ¹⁷	80	24	Gammacell® 220 ² (NORDION)	Co-60
USA (Hawaii)	<i>Ceratitis capitata</i>	140	47	Husman 521 ² (2 units) (ISOMEDIX)	Cs-137
USA (Texas)	<i>Anastrepha ludens</i>	70	38	Husman 521 ² (ISOMEDIX)	Cs-137

¹Sterility-inducing dose in hypoxia (except *Cydia pomonella*)²Self-contained dry-storage irradiator³Panoramic irradiator⁴*C. capitata* (Wiedemann)⁵*Ae. aegypti* (L.)⁶*G. palpalis gambiensis* Vanderplank⁷*C. pomonella* (L.)⁸*Ae. albopictus* (Skuse)⁹*A. ludens* (Loew)¹⁰*B. oleae* (Rossi)¹¹*C. formicarius* (F.)¹²*E. postfasciatus* (Fairmaire)¹³*A. obliqua* (Macquart)¹⁴*C. hominivorax* (Coquerel)¹⁵*B. dorsalis* (Hendel)¹⁶*T. leucotreta* (Meyrick)¹⁷*B. correcta* (Bezzi)

In recent years, because of the potential use of radionuclides in terrorist attacks, governments and the International Atomic Energy Agency (IAEA 2012, 2017) have encouraged the development of alternatives to gamma irradiators. Governmental and international controls on radioactive materials have increased the difficulty and expense of purchasing, transporting, or reloading gamma irradiators. In addition, in many jurisdictions, facilities with gamma sources are required to have comprehensive and expensive security systems that include such features as 24-h video monitoring, motion and tamper sensors, and access systems that incorporate multi-factor recognition of users. Users with unescorted access to the facilities are now often required to pass extensive background checks.

On the other hand, X-ray irradiators have the advantage that they can easily be shipped internationally, and only need access to electricity and the replacement of X-ray tubes after every few thousand hours of use. Nevertheless, their use can be energy-intensive, and experience thus far indicates that they require more maintenance, and are less reliable for continuous operation, than gamma irradiators (IAEA 2012).

3.2. Radiation Safety

It is essential that written descriptions of specific safety procedures, for all activities at an irradiation facility, are prepared. Before using a radiation source, workers must be given detailed training on relevant national legislation and regulations, and on safety procedures for the installation and use of a radiation source (IAEA 2003, 2014).

Irradiators are designed to keep the radiation exposure and dose to workers “as low as reasonably achievable” (ALARA), and within pre-set limits. These dose limits are based on the recommendations of several agencies of the United Nations (UN), including the IAEA, Food and Agriculture Organization of the United Nations (FAO), and World Health Organization (WHO) (IAEA 2014). Appropriate safety methods and procedures have been developed for each type of irradiator, and when operated correctly with the appropriate safeguards, they are safe and easy to use. Irradiators are usually licensed by national atomic energy authorities which set certain requirements, such as restricting access (entry for authorized persons only), a periodic survey of the radiation field in the vicinity where workers could be present, the use of personal radiation dosimeters, and the availability of radiation survey meters. These requirements are specifically aimed at protecting all workers from radiation. In addition, irradiators incorporate interlocks that prevent unintentional access to areas with high radiation fields. Cases of accidental exposure to Co-60 gamma rays are usually reported by the IAEA (IAEA 1996; Gonzalez 1999), and data from such historic cases are useful for probabilistic risk assessment. When the useful life of a gamma source is over, the irradiator or the source pencils are usually returned to the supplier for storage, reuse, recycling, or disposal. This is now becoming a mandatory and elaborate procedure.

During handling of insects, especially adult Lepidoptera, irradiator operators may be exposed to insect allergens, and additional safety measures may be required to minimize the risk of allergy and health hazards (Parker, Mamai et al., this volume).

3.3. *Measurement and Distribution of Absorbed Dose*

3.3.1. *Radiation Dosimetry*

For the success of a programme using the SIT, the absorbed dose delivered to the insects needs to be accurately measured and controlled. Also, if contractual arrangements or national regulations prescribe specific doses, the programme will require adequate means to demonstrate compliance. Therefore, the programmes need to have an established system to accurately measure absorbed dose and estimate the associated confidence interval, a process known as dosimetry (ISO/ASTM 2013a). Dosimetry is performed using dosimeters — devices that, when irradiated, exhibit a quantifiable change in some property, e.g. colour, that can be related to the absorbed dose. A dosimetry system includes dosimeters (that are placed in different positions within the canister), measuring instruments (to read the change in the dosimeters) along with their associated reference standards, and procedures for using them (ISO/ASTM 2013b).

Dosimeters are commonly used in sterile insect production facilities for tasks such as absorbed-dose mapping (section 3.3.2.), qualification of the irradiator (section 3.5.2.), and process control (section 3.5.3.). Several dosimeters are suitable for these routine dosimetry procedures at SIT facilities (ISO/ASTM 2013a). Many facilities use radiochromic film systems because they are relatively affordable and are simple to use (avoiding extensive training) (IAEA 2004). Procedures for calibrating routine dosimetry systems, and for determining radiation fields in irradiators used for insect sterilization, are described in various ISO/ASTM standards (section 3.5.1.) (ISO/ASTM 2009; 2013a, b, c), which are updated periodically, and in an IAEA technical report (IAEA 2002b). Reference-standard dosimeters are used to calibrate the routine dosimetry system, and to determine the dose rate at a reference position in a self-contained irradiator. Sterile insect production facilities use reference-standard dosimeters for both of these purposes. Accredited dosimetry laboratories typically provide these dosimeters and make the readings, resulting in measurements that are “traceable” to national or international standards.

3.3.2. *Absorbed-Dose Mapping*

Ideally, it would be desirable to irradiate all insects in a container (or a canister) at the same dose. In practice, because of the characteristic of radiation interaction with matter, there is a systematic pattern of dose variation within the canister, and therefore not all insects receive the same dose. Dose distribution within the canister is determined by “dose mapping”, which typically is conducted by placing several dosimeters at known locations throughout the canister. Dose mapping provides operators of SIT irradiators with information on the absorbed dose within the canister, including areas of maximum and minimum dose, the dose uniformity ratio (maximum dose/minimum dose), and areas where the dose rate is relatively uniform (Fig. 4). Techniques for dose mapping are described in detail in Walker et al. (1997) and ISO/ASTM (2013a).

Figure 4. Example of isodose curves in the irradiation chamber of a Gammacell® 220. Values are normalized to 100 in the centre of the gamma field. The field is most uniform in the centre. In this case the dose uniformity ratio (DUR) is 1.5 [120/80]. Grid is at 2-cm intervals from the centre of the chamber. (Figure from MDS Nordion, reproduced with permission.)

3.4. Radiation Sterilization of Insects

3.4.1. Selecting Sterilizing Dose

The dose that is used to induce sterility is of prime importance to programmes that release sterile insects. As the absorbed dose increases, sterility increases, but insect

quality and competitiveness will decrease (Parker, Vreysen et al., this volume; Lance and McInnis, this volume). Insects that receive too low a dose are not sufficiently sterile, and those that receive too high a dose will be non-competitive, reducing the effectiveness of the programme. Quite often, full (100%) sterility is not the most favourable condition for a programme, and thus process optimization is necessary to balance sterility level and competitiveness, taking into consideration factors that could affect the radiation sensitivity of insects (section 4.) and programme requirements (Parker and Mehta 2007). If quarantine security is a consideration, 100% sterility may be required for any released females. Males, however, tend to be less radiosensitive, and, in many species, eliminating a residual egg hatch of 1% (or less) from fertile females mated to irradiated males (even though many of these eggs do not survive other stages) requires doses that substantially reduce the ability of males to compete with, and thus induce sterility into, wild populations (Fisher 1997; Toledo et al. 2004).

Therefore, given the unavoidable dose variability within a canister (as mentioned above), sterile insect production facilities define an acceptable range of doses that can be given to the insects. Most often, programmes or regulatory officials specify a minimum dose that all insects must receive to ensure sufficient sterility. Due to dose variability, most insects actually receive a dose that is somewhat higher than that minimum. An alternate approach is to specify an optimum (or central target) dose, and set this as the average or median dose within the irradiated volume of insects. In either case, the dose uniformity ratio (DUR) should be small, preferably below 1.3. The goal is to sterilize all insects sufficiently without treating large proportions with doses that are too high, substantially reducing competitiveness. Irradiator operators can often adjust process parameters to achieve a more uniform dose distribution (section 3.5.2.).

Induced mutations may exert lethality at any stage of insect development. Quite often, for reasons of simplicity and convenience, the induction of detrimental lethal mutations is measured solely on the basis of egg hatchability. However, because lethal mutations can affect any developmental stage, researchers should measure dose effects all along this developmental continuum, or the actual survivorship from egg to adult, to give a true picture of induced sterility. As a result, 99 or 100% sterility in the egg stage is not essential nor desirable if it drastically reduces the competitiveness and vigour of the sterile insect. In some moths, the F_1 generation is more sterile than the substerilized parent generation. These are unique genetic phenomena in more radiation-tolerant species that are responsible for inherited sterility (IS) in Lepidoptera and some other arthropods (Marec et al., this volume).

An informed decision on treatment dose requires accurate data on how factors such as dose, insect stage and age, and various process parameters affect levels of sterility and insect quality. For programmes that apply the SIT, the accuracy and value of such data depend on the use of standardized dosimetry systems, procedures, and reporting methods (ISO/ASTM 2013a; FAO/IAEA/USDA 2019). Published data on the radiation biology of the same or similar species can provide guidance, but, in many cases, are of limited value because dosimetric procedures, dose-measurement traceability, dose distribution, and other pertinent information are often not reported. In addition, the details of insect-handling procedures, and, perhaps, strain-related differences, can influence radiation sensitivity (section 4.).

3.4.2. *Preparing Insects for Irradiation*

Stage/Age of Insects. The selection of the insect development stage and age at which the insects will be irradiated is based on knowledge of the timing of maturity of insect reproductive organs (section 4.2.), handling suitability during irradiation and subsequent shipping, and sensitivity to somatic damage. For many holometabolous species (having complete metamorphosis), a good time for irradiation is late in the pupal stage, or early in the adult stage, when germ tissues have formed (Anwar et al. 1971; Ohinata et al. 1971, 1977, 1978). For example, tephritid flies are usually irradiated 1 or 2 days prior to adult emergence (pupae kept at about 25°C). Flies that are irradiated earlier in the pupal stage will tend to be of lower quality (in terms of mating propensity, flight, and sex pheromone production), an indication that somatic tissues were adversely affected (Fletcher and Giannakakis 1973). However, when tephritid pupae are irradiated too close to adult emergence, a proportion of females can already have some developed oocytes that, in spite of having been irradiated, can become viable eggs (Williamson et al. 1985). Ideally, the development and maturity stage should show an external physical indicator that acts as a quick and reliable identification tool, such as pupal eye-pigment colour in the Mediterranean fruit fly (Ruhm and Calkins 1981; Seo et al. 1987; Resilva and Pereira 2014).

In the pentatomid bug *Nezara viridula* (L.), sexual maturity and mating occur 5–17 days after adult emergence. Fourth- and fifth-instar nymphs are most frequently selected for irradiation because they are more radiosensitive than adults, and male and female reproductive systems are already well developed at this stage (Kiritani 1963; Mitchell and Mau 1969).

Packaging for Irradiation. Insects are usually irradiated in the primary packaging containers that are subsequently transferred, unopened, to an emergence and release facility where the adult insects are prepared for release (FAO/IAEA 2017). These containers provide protection to the sterile insects, and guard against their escape. They also prevent tampering. A variety of packaging containers has been used, e.g. 2- and 4-litre polyethylene bags, unwaxed paper cups (with lids), paper boxes, and plastic bottles of up to 15-litre capacity. SIT irradiation protocols may incorporate reusable canisters (typically steel, aluminium or plastic) that hold the primary packaging containers during irradiation. The size and shape of these canisters are usually a function of the size and shape of the irradiation chamber, especially in the case of self-contained irradiators (section 3.5.2.).

If insects are irradiated in a reduced-oxygen atmosphere, as a means of reducing the formation of free radicals (section 4.1.), the packaging container must be airtight. For example, tephritid pupae are sealed, with as little air space as possible, in plastic bags or bottles and then held at cool temperatures (12–20°C) for at least 1 hour before irradiation. During this period the insects exhaust most of the oxygen remaining within the container. Hypoxia (a deficiency of oxygen reaching the tissues of the body) can also be achieved by saturating the atmosphere within the container with helium or, more commonly, nitrogen, prior to and during irradiation (Ashraf et al. 1975; Ohinata et al. 1977, 1978; Hooper 1989).

3.5. *Quality Assurance*

3.5.1. *Quality Assurance Programmes*

Quality assurance (QA) is an important part of any successful AW-IPM programme using the SIT. A QA programme provides various benefits with respect to irradiation procedures, including:

- Success of the process — adequately sterilized insects of good quality can be produced consistently,
- Compliance with regulations — a QA programme makes it convenient to audit the process against established standards,
- Harmonization — as international trade of sterile insects is growing, it has become more important to ensure dependable uniformity across geographical and political regions,
- Public acceptance — when the public realizes that SIT facilities strictly follow set procedures and document the process, it has more confidence in the programme.

An effective QA programme includes standard operating procedures (SOPs) for all activities related to packaging, irradiation, and dosimetry. Also, processing equipment that controls key operating parameters (those affecting dose) is periodically tested and/or calibrated to verify that the irradiator is operating properly. This is then documented as part of the record for the QA programme.

For many processes related to insect sterilization using radiation, standards and guidelines are available that can be incorporated into a facility's QA programme. These include dosimetry standards developed by the International Organization of Standardization and the American Society for Testing and Materials (ISO/ASTM 2009, 2013a, b, c, d), an SOP for using the Gafchromic® film dosimetry system for the SIT (IAEA 2004), and a comprehensive quality-control manual for applying the SIT against fruit flies (FAO/IAEA/USDA 2019).

3.5.2. *Irradiator Operation and Configuration*

When an irradiator is installed, it is evaluated to ensure that it is working according to the manufacturer's specifications, and baseline data on its performance are developed. These two activities are known as *installation qualification* and *operational qualification*, respectively (ISO/ASTM 2013a). Operational qualification includes, among other things, initial dose mapping (section 3.3.2.), and measurement of the dose rate at a reference position, e.g. at the centre of a fully filled canister (section 3.3.1.). The reference dose rate is then used to establish the basic relationship between key operating parameters, such as timer setting or conveyor speed, and absorbed dose. Dosimetry standards recommend repeating periodically the reference dose-rate measurement, e.g. every 3 years for gamma irradiators (ISO/ASTM 2013a). A caesium-137 (Cs-137) source, in particular, may contain impurities (Cs-134) that affect the decay rate, and thus, over time, the dose rate. For the low-energy X-ray irradiators, it is recommended that the reference dose rate be measured annually. Reference-standard dosimetry and dose mapping are repeated as appropriate following any changes in the irradiator, such as source renewal in gamma irradiators or a new X-ray tube, which could affect the dose rate or dose distribution.

Before insects are sterilized, key process parameters are established as part of performance qualification. For most insect irradiators, the absorbed dose delivered to the insects is controlled by adjusting a single parameter, such as timer setting (irradiation time) or conveyor speed. For X-ray irradiators, the absorbed dose also depends on the tube voltage and tube current. Values of these parameters depend on the dose specifications (section 3.4.1.) and the reference dose rate on the day of irradiation. Dose mapping is again performed to ensure that all insects within a given canister will receive an appropriate dose. If necessary, process parameters can often be adjusted to improve dose uniformity; common alterations include optimizing the size or shape of the canister, rotating the canister on a turntable during irradiation, using dose attenuators, and using plugs of simulated product, e.g. styrofoam, in the canister or irradiation chamber to exclude insects from areas with unacceptably low or high dose rates. This procedure establishes a canister design and a loading configuration of insects that result in an acceptably uniform dose distribution, and if possible reduce the DUR to 1.3 or less. If any of the changes listed above are made to improve dose uniformity, dose mapping should be repeated. The results of this mapping may also be used to establish a reference location for performing routine dosimetry as part of process control (section 3.5.3.).

3.5.3. Process Control

The accidental release of insects that are not irradiated properly could potentially be disastrous (Knippling 1982; FAO/IAEA 2017), especially in programmes like those in California and Florida, USA, where the SIT is used to eradicate extremely small pest populations and/or as a prophylactic measure to prevent the establishment of newly introduced pests. To avoid this problem, programmes that release sterile insects implement various process-control elements to help ensure that all insects are irradiated according to specifications (FAO/IAEA/USDA 2019). In addition to the elements listed below, programmes applying the SIT often monitor relevant process parameters such as those related to the preparation and packaging of insects, setting of the irradiator timer, conveyor speed, canister specifications, and position and loading of the canisters. The results of process monitoring are routinely documented as part of the record of the QA programme.

Sterility Testing. Most AW-IPM programmes that integrate the SIT test samples of irradiated insects on a regularly scheduled basis to confirm that specified levels of sterility are being achieved. The quality-control manual for using the SIT against fruit flies suggests that this could be done for every shipment (FAO/IAEA/USDA 2019), comparing the egg hatch from pairings of irradiated and non-irradiated insects with that from crosses of non-irradiated insects. Besides making regularly scheduled sterility tests, unscheduled tests should also be conducted before any insects are shipped whenever changes are made to any equipment or procedures. However, it takes time to obtain the results of a sterility test, and the results may be known too late to prevent the release of incorrectly treated insects. Therefore, sterility testing must be supplemented with other methods, such as routine dosimetry.

In addition, the competitiveness of the sterile insects needs to be checked with insects of the target population to ensure the efficacy of the programme. Such testing helps to ensure that all procedures are being followed correctly, including rearing, pre-irradiation preparation (e.g. age-based selection of insects), packaging for hypoxia or nitrogen (if used), temperature control, irradiation-dose control, and post-irradiation handling (FAO/IAEA 2017).

Routine Dosimetry. Regular dosimetry can help to confirm that insects are being irradiated according to programme specifications, and may be required for every shipment (FAO/IAEA/USDA 2019). This is usually done by placing dosimeters on packaging containers or canisters at a specific location (which may be the reference location identified through dose mapping performed during performance qualification (section 3.5.2.)), where the dose rate has a known and predictable relationship to the minimum and maximum dose rate within those canisters. Unlike sterility testing, routine dosimetry can identify problems in the irradiation process quickly enough so that improperly sterilized batches of insects can be intercepted prior to release in the field. Although routine dosimetry is faster than sterility testing, a third control described below provides an immediate visual confirmation check that a given container has gone through the irradiation process.

Radiation-Sensitive Indicators. A radiation-sensitive indicator is a material, such as a coated or impregnated adhesive-backed (or adhesive-fronted) substrate, ink, or coating that undergoes a qualitative visual change when exposed to a specified dose of radiation (ISO/ASTM 2013d). The dose at which the indicator changes should ideally be below, but near, the minimum dose required for the sterilization process. Since the degree of colour change is not proportional to the dose, these indicators cannot substitute for dosimeters.

Indicators are used as aids in tracking whether or not specific containers have been irradiated (Fig. 5). The relevant manuals (FAO/IAEA 2017; FAO/IAEA/USDA 2019) suggest that an indicator should be attached to each packaging container of sterile insects to help ensure (along with product segregation protocols and other procedural methods) that non-irradiated insects are not unintentionally released in the field. Also, indicators could potentially be used to assist in tracking multiple passes of containers through an irradiator when the sterilizing dose is fractionated into several smaller doses (section 4.1.).

Indicators that are exposed to excessive humidity, high temperature or UV radiation, e.g. sunlight, before or after irradiation may give erroneous readings; hence they are useful only within an irradiation facility where these conditions are controlled.

Recommended dosimetric procedures, including routine dosimetry and the use of indicators for programmes releasing sterile insects, are described in published standards and guides, e.g. ISO/ASTM 2013a, c, d; FAO/IAEA/USDA 2019.

Figure 5. Radiation-sensitive indicators before (upper) and after (lower) exposure at dose >125Gy (© ISP 2002). (Figure from FAO/IAEA/USDA 2019.)

4. FACTORS MODIFYING INSECT RADIATION SENSITIVITY

The sensitivity of arthropods to radiation depends on many parameters. Radiation sensitivity varies widely among species (section 6.), but environmental conditions, and the biological state of the organism at the time of irradiation, also can have significant influences. These latter factors should be optimized so that sterilized insects are of the highest possible quality.

4.1. Environmental and Physical Factors

4.1.1. Ambient Atmosphere

Oxygen levels affect the sensitivity of insects to radiation (Baldwin and Chant 1971; Economopoulos 1977; Ohinata et al. 1977; Rananavare et al. 1991; Fisher 1997). Damage induced by radiation is typically lower in an oxygen-reduced environment (hypoxia) than in air, so usually higher doses are needed to produce comparable reproductive sterility. However, because the magnitude of this protective effect tends to be greater for somatic damage than sterility, the use of oxygen-reduced atmospheres is a common strategy to improve sterile insect competitiveness without sacrificing sterility (Parker, Vreysen et al., this volume; Lance and McInnis, this volume). Methods for inducing hypoxia are described in section 3.4.2.

The increased radiation damage in a high-oxygen environment is a general phenomenon in radiobiology. Ionizing radiation initiates a chain of oxidative reactions along the radiation path in the tissues and the formation of simple free radicals (H^0 or OH^0) with very short lifetimes on the order of 10^{-10} sec, which in the absence of dissolved oxygen might be neutralized by combining with hydrogen radicals resulting in no net damage. In the presence of dissolved oxygen, damaging peroxy-radicals (HO_2^0 or RO_2^0), free radical species with greater stability and

lifetimes, may be formed that irreversibly alter the organic molecules, including the germ cell chromosomes (Tubiana et al. 1990). For the protective effect of low oxygen to be seen, the tissues must be under anoxic or hypoxic conditioning prior to and during irradiation. Anoxic conditioning of adults prior to emergence led to an increase in antioxidant capacity driven by mitochondrial superoxide dismutase and glutathione peroxidase. When exposed to gamma irradiation, a strong oxidative stressor, males that received anoxic conditioning had lower lipid and protein oxidative damage at sexual maturity (López-Martínez and Hahn 2012). It must be noted that high-LET radiation (e.g. alphas, neutrons) is less affected by the presence or absence of oxygen than low-LET radiation (X-rays and gamma radiation). This may be because high-LET radiation causes several ionizations within one macromolecule, damaging it beyond repair (Pizzarello and Witcofski 1967).

4.1.2. Dose Rate

The adverse effects of radiation appear, in general, to be lessened by reducing the rate at which the sterilizing dose is delivered to the insects. This can be done by using a lower dose rate, and longer irradiation time, for a single irradiation (Yanders 1959; Nair and Subramanyam 1963; Hooper 1975; Mayas 1975; Ilao 1977).

An alternate approach to conserve insect quality is dose fractionation, where the sterilizing dose is delivered over time in a series of smaller irradiations (North 1975; LaChance and Graham 1984; Haynes 1993; Tamhankar and Shantharam 2001). However, because of its impracticality, current AW-IPM programmes applying the SIT usually do not follow this procedure (although see Kumano et al. 2012).

4.1.3. Temperature

There are some data to suggest that irradiation at reduced temperatures tends to reduce the sensitivity of arthropods to radiation (Rananavare et al. 1991). Low temperatures, to a certain limit, and hypoxia, also reduce the metabolic rate, and therefore the development rate of insects during irradiation. However, temperature does not affect the actual dose delivered to the insect.

4.2. Biological Factors

4.2.1. Cell Stage and Characteristics

The most radiosensitive cells are those (1) with a high mitotic rate, (2) with a long mitotic future (i.e. under normal circumstances, they will undergo many divisions), and (3) which are of a primitive type. These generalizations, with some exceptions, have become known as the Law of Bergonie and Tribondeau (Casarett 1968). In this regard, germ cells are the most radiosensitive, and show different killing and sterilization susceptibility according to their development stage.

It is generally accepted that chromosomal damage (structural and numerical anomalies) is the cause of dominant lethal mutations. Dominant lethal mutations occurring in a germ cell do not cause dysfunction of the gamete, but are lethal to the fertilized egg or developing embryo (Robinson, this volume). The earlier stages of

spermatogenesis (spermatocytes and spermatogonia) are generally more radiosensitive than later stages (spermatids and spermatozoa) (Proverbs 1969). Dey and Manna (1983) found that chromosomes in spermatogonial metaphase and anaphase I were more sensitive to X-rays than those in other stages. Germ-cell sensitivity in female insects is, however, complicated by the presence of nurse cells that are most susceptible to injury during mitosis (LaChance and Leverich 1962).

The dose required to inhibit mitosis is reported to be inversely proportional to the number of chromosomes, and correlates with the average interphase chromosome volume. The larger the nuclear volume, apparently the greater is the sensitivity. Similar relationships were determined in animals and plants, and used to predict their sensitivity to chronic irradiation (Sparrow et al. 1963, 1967; Casarett 1968; Whicker and Schultz 1982; Jacquet and Leonard 1983). Furthermore, radiosensitivity appears to be influenced by additional parameters including cell repopulation capacity, tissue and organ regeneration ability, and biological repair (Harrison and Anderson 1996).

Chromosome organization can also affect the response to radiation. Several insect orders (Hemiptera, Lepidoptera, Trichoptera, Odonata, and Dermaptera) have holokinetic chromosomes, i.e. properties of the centromere are distributed over the entire chromosome (Kuznetsova and Chubareva 1979; Marec et al., this volume). LaChance and Riemann (1973) suggested that, in these taxa, most dominant lethal mutations cause death after blastoderm formation. In other orders, dominant lethal mutations are expressed during the early cleavage divisions.

4.2.2. *Developmental Stage and Age*

Age and developmental stage are important parameters to be taken into consideration when deciding on radiation process parameters for the SIT. In general, adults are less radiosensitive than pupae, which in turn are less sensitive than larvae. Similarly, older pupae tend to be less sensitive to radiation than younger pupae (Ismail et al. 1987; Ahmed et al. 1990; Hamed and Khattak 1991; Dongre et al. 1997). Also, there is a negative relationship between the age of eggs and their sensitivity to radiation (Chand and Sehgal 1978).

4.2.3. *Gender*

Regarding sterilization or disinfestation, female arthropods are, in general, more radiosensitive than males (Cogburn et al. 1973; Hooper 1989; Hallman 1998), but there are numerous exceptions. For example, males were found to be more radiosensitive than females in the hemipteran families Pyrrhocoridae, Piesmididae, and Pentatomidae (Mau et al. 1967), the American cockroach *Periplaneta americana* (L.) (Wharton and Wharton 1959), certain Coleoptera (section 6.2.), and ixodid ticks (Purnell et al. 1972).

The wide variation reported among species in relative radiosensitivity of males versus females likely results in part from differences in the maturity of oocytes present when females are irradiated. For example, if Mediterranean fruit fly female pupae are irradiated one or two days before adult emergence, egg production is completely stopped by doses well below those needed to sterilize males. However, on the day before emergence and at later times, females contain increasing numbers of

oocytes that mature into viable eggs even if irradiated at doses sufficient to sterilize males (Williamson et al. 1985).

4.2.4. Size and Weight

Early studies (Wharton and Wharton 1957; Willard and Cherry 1975) suggested that species with large adults tend to be more radiosensitive than those with small adults. Experiments have shown that the American cockroach *Periplaneta americana* (L.) is killed or sterilized by radiation doses to which smaller insects such as *Drosophila*, *Habrobracon*, and *Tribolium* are much less sensitive (Lanouette et al. 2017; Krüger et al. 2018). Similarly, other studies (Cole et al. 1959) found that the LD-50 varied inversely with the size of the insect species tested (body louse *Pediculus humanus humanus* L., house fly *Musca domestica* L., *Periplaneta americana*, German cockroach *Blattella germanica* (L.), firebrat *Thermobia domestica* (Packard), bed bug *Cimex lectularius* L., and Pharaoh ant *Monomorium pharaonis* (L.)). However, the correlation between size, weight, and radiosensitivity has not proved to be strong.

4.2.5. Diapause

The effects of diapause on insect sensitivity to radiation appear to vary. Mansour (2003) found that radiation-related reductions in adult emergence were greater following treatment of diapausing than that of non-diapausing larvae of the codling moth *Cydia pomonella* (L.), but other authors reported that diapausing and non-diapausing larvae of other species were equally sensitive to radiation (Ignatowicz 1997; Hallman 2000). Carpenter and Gross (1989) reported no interaction between inherited sterility (IS) and diapause with regard to several traits, although crosses involving moths that emerged from diapaused F₁ pupae produced significantly fewer eggs. In contrast, diapausing twospotted spider mites *Tetranychus urticae* Koch appeared more tolerant to radiation than non-diapausing mites (Lester and Petry 1995).

4.2.6. Nutritional State

Pre- or post-irradiation starvation, or the nutritional state, may influence radiosensitivity (Wharton and Wharton 1959; Stahler and Terzian 1963; Drummond et al. 1966). For example, to achieve 100% sterility, male and female lone star ticks *Amblyomma americanum* (L.) required about 10 Gy before engorgement and 24 Gy after engorgement (Drummond et al. 1966). The data suggested an attenuation of radiation-induced lethality in a blood-fed organism, but the mechanism remains unknown. Beuthner (1975) did not find such differences in *Amblyomma variegatum* (F.), *Hyalomma anatolicum excavatum* Koch or *Rhipicephalus appendiculatus* Neumann.

4.2.7. Additional Factors

An insect's state of hydration, or moisture content, could potentially influence the effects of radiation, but probably this is applicable mostly to commodity disinfestation. Diurnal rhythms apparently can influence the induction of sterility by

radiation. Rananavare et al. (1991) found that potato tuberworms *Phthorimaea operculella* (Zeller) irradiated in scotophase were more sensitive than those treated in photophase. Finally, genetic differences related to geographical diversity within a species can potentially affect insect radiosensitivity (Fisher 1997; Hallman 2003; Azizyan and Ter-Hovhannesian 2010).

Enterobacter spp. and other bacterial strains as probiotics can be useful where irradiation affects insect fitness. Probiotics in diets greatly improved various fitness parameters in irradiated insects, including pupal weight, longevity, adult size, flight ability, and adult emergence. Also, in terms of mating competitiveness, irradiated males reared on probiotics achieved more matings and transferred larger quantities of sperm to females (Stathopoulou et al. 2021; Augustinos et al., this volume).

5. ARTHROPOD SPECIES SUBJECTED TO RADIOSTERILIZATION

The International Database on Insect Disinfestation and Sterilization (IDIDAS) (Bakri et al. 2005; IDIDAS 2018) was developed to collect and share information about radiation doses for disinfestation and reproductive sterilization of arthropods, and to perform a comparative analysis and quality-assurance check on existing data. IDIDAS was based on a literature review and analysis of more than 5330 references that were published during the past six decades. Due to space limitations, these references are not included here but are available on the IDIDAS website (Fig. 6).

Figure 6. Home page of the International Database on Insect Disinfestation and Sterilization that provides doses required for the phytosanitary irradiation of infested commodities, as well as for the induction of sterility, in more than 360 arthropod species (IDIDAS 2018).

In the past six decades, at least 360 species of arthropods of economic importance, belonging to 216 genera, 83 families, 8 insect orders and 2 arachnid orders, have been subjected to irradiation studies for the purposes of research, biological control, or pest management programmes (Table 3). Of these, 29% are Diptera, 24% Coleoptera, 24% Lepidoptera, 9% Hemiptera, 7% Acari, 3% Thysanoptera, 1.5% Hymenoptera, 1% Blattodea, 1% Araneae, and less than 1% Orthoptera and Phthiraptera. Out of 101 entries on Diptera from 17 families and 32 genera, 41 species belong to the Tephritidae; this group is important in pest management and international trade. The Curculionidae (Coleoptera), Tortricidae and Pyralidae (Lepidoptera), and Culicidae (Diptera) follow Tephritidae in the number of species radiosterilized.

Potential sources of error in any compilation of records, such as this database, are numerous. One of the main difficulties derives from taxonomy, an evolving science; during the past 60 years the names of many pest species, families and orders have been revised. In some taxa, e.g. Blaberidae, the mean radiation dose with a large confidence limit range raises questions about the source of the error.

Organisms for irradiation drawn from a cultured population should, therefore, be defined for posterity by lodging voucher specimens in an appropriately secure and curated collection. This is particularly important for groups subject to frequent taxonomic changes, such as the Tephritidae.

6. RADIATION DOSES FOR ARTHROPOD STERILIZATION

Arthropods are less radiosensitive than humans and other higher vertebrates (Table 4), but more sensitive than viruses, protozoa and bacteria (Ravera 1967; Rice and Baptist 1974; Whicker and Schultz 1982; Blaylock et al. 1996; Harrison and Anderson 1996). One of the main reasons for the lower radiosensitivity is that arthropods have a discontinuous growth during immature stages, and cells become active only during the moulting and metamorphosis processes. This is encoded in Dyar's Rule, i.e. insects double their weight at each moult and thus their cells need to divide only once per moulting cycle (Hutchinson et al. 1997; Behera et al. 1999). The low sensitivity of most adult insects to radiation is attributed to the fact that they are composed of differentiated cells, which do not undergo replacement (Sullivan and Grosch 1953). Such cells are much more resistant to death or damage induced by irradiation than are dividing or undifferentiated cells.

Radiation doses for sterilization (Table 3), as reported in the literature (IDIDAS 2018), were summarized using similar criteria. In general, the developmental stage irradiated was the pupa, but for some groups data are available only for eggs, larvae or adults. Other experimental parameters such as temperature, radiation source, dose rate, etc., may have differed. Even compiling the data was difficult because of the absence of uniform experimental procedures and dosimetry, and the influence of various parameters. Dose values reported below may also differ from doses that are routinely used to sterilize members of the reported taxa for the SIT, especially in cases where programmes irradiate insects in oxygen-reduced atmospheres. Therefore, the dose ranges presented should be considered only as guidelines for further investigation and to provide general introductory information (Bakri and Hendrichs 2004; Bakri et al. 2005).

Table 3. Calculated mean and 95% confidence limits (upper L_2 , lower L_1) (Sokal and Rohlf 1995) for radiosterilization doses for insects and other arthropods. Data are for in-air irradiation of males treated mostly as pupae (or eggs, nymphs, adults as indicated). Other factors, e.g. radiation source, temperature, dose rate, and level of sterility achieved, are not necessarily consistent. (References for data from IDIDAS 2018)

Order	Family	Number of genera	Number of species	Sterilization dose (Gy)		
				L_2	Mean	L_1
Acari	Acaridae	4	5	516	375	233
	Argasidae	2	2	20	20	20
	Dermanyssidae (Nymph)	1	1	7.5	7.5	7.5
	Eriophyidae (Adult)	4	4	350	350	350
	Ixodidae	4	7	23	20	16
	Oligonychidae (Adult)	1	1	200	200	200
	Tenuipalpidae	1	3	300	300	300
	Tetranychidae	2	4	300	300	300
Araneae	Araneidae	1	1	40	40	40
	Eresidae (Adult)	1	1	150	150	150
	Pholcidae (Adult)	1	1	20	20	20
Blattodea	Blaberidae (Adult)*	2	2	205	72	-60
	Ectobiidae	1	1	32	32	32
Coleoptera	Anobiidae (Adult)	3	3	70	43	17
	Bostrichidae (Adult)	2	2	165	155	145
	Bruchidae	3	6	77	55	33
	Cerambycidae (Adult)	1	1	90	80	70
	Chrysomelidae (Adult)	3	3	28	28	28
	Coccinellidae	1	1	35	35	35
	Curculionidae (Adult)	21	29	71	54	38
	Dermestidae (Adult)	3	8	227	170	113
	Elateridae (Adult)	1	1	100	80	60
	Laemophloeidae (Adult)	1	3	200	200	200
	Lyctidae (Adult)	1	1	69	69	69
	Nitidulidae	1	1	75	75	75
	Ptinidae	1	1	300	300	300
	Scarabaeidae	5	5	111	72	33
	Scolytidae	1	2	69	43	18
	Silvanidae	2	3	117	117	117
	Tenebrionidae	8	15	186	140	94
Diptera	Agromyzidae	1	2	162	158	152
	Anthomyiidae	1	2	45	35	38
	Calliphoridae	3	5	32	30	18
	Ceratopogonidae**	1	1	300	300	300

Table 3. Continued

Order	Family	Number of genera	Number of species	Sterilization dose (Gy)		
				L_2	Mean	L_1
Diptera	Chironomidae (Egg)	1	1	1000	1000	1000
	Chloropidae	1	1	38	38	38
	Culicidae	3	17	175	80	118
	Drosophilidae	1	6	179	140	100
	Glossinidae (Adult)	1	11	117	85	53
	Muscidae	4	6	31	25	19
	Oestridae	2	3	52	45	38
	Piophilidae	1	1	100	100	100
	Psilidae	1	1	43	43	43
	Sarcophagidae	1	1	52	36	19
	Sciaridae (Adult)	1	1	40	40	40
	Tachinidae	1	1	20	20	20
	Tephritidae	8	41	108	85	83
Hemiptera	Aleyrodidae (Nymph)	3	4	72	70	58
	Aphididae (Adult)	3	3	283	140	198
	Cicadellidae (Adult)	1	1	200	180	160
	Coccidae (Nymph)	1	1	250	250	250
	Coreidae (Adult)	2	2	80	80	80
	Delphacidae	2	2	118	81	44
	Diaspididae (Adult f.)	4	4	234	185	136
	Lygaeidae (Adult)	1	1	100	100	100
	Miridae (Adult)	1	2	200	200	200
	Pentatomidae (Adult)	3	4	62	55	48
	Pseudococcidae	4	5	183	125	148
	Pyrhocoridae	1	1	70	70	70
	Reduviidae	3	3	90	70	50
Hymenoptera	Apidae	1	1	109	90	70
	Formicidae	4	5	92	80	67
Lepidoptera	Arctiidae (Adult)	2	2	430	350	270
	Bombycidae (Adult)	1	2	250	250	250
	Elachistidae (Adult)	1	1	200	200	200
	Crambidae	6	10	385	275	165
	Gelechiidae (Adult)	5	5	303	213	123
	Gracillariidae	1	1	450	450	450
	Lymantriidae	2	2	257	230	158
	Lyonetiidae	1	1	900	900	900
	Noctuidae	6	14	611	400	188
	Pieridae	1	1	350	350	350

Table 3. Continued

Order	Family	Number of genera	Number of species	Sterilization dose (Gy)		
				L_2	Mean	L_1
Lepidoptera	Plutellidae	1	1	200	200	200
	Pyalidae	9	18	522	363	203
	Sphingidae	1	1	100	100	100
	Thaumetopoeidae	1	1	40	40	40
	Tineidae	2	2	120	120	120
	Tortricidae	19	22	452	375	298
Orthoptera	Acrididae	1	1	4	4	4
Phthiraptera	Pediculidae	1	1	750	750	750
Thysanoptera	Phlaeothripidae	1	1	200	200	200
	Thripidae	5	9	200	200	200

*Blaberidae: Questionable in view of very large confidence limit range

**Fertility recovery after first mating

(Adult f.) = Adult female

Table 4. Ranges of LD_{50} for acute irradiation of organisms from different taxonomic groups (length of time for survival is usually set at 30 days for mammals, but longer times may be needed for other organisms) (Table from Bakri et al. 2005, reproduced with permission)

Group	LD_{50} (Gy)	Reference
Bacteria, protozoa, viruses	100–10 000	Harrison and Anderson 1996
Insects	30–1500	Whicker and Schultz 1982
Molluscs	50–500	Ravera 1967
Higher plants	1.5–>130	Harrison and Anderson 1996
Fish	4–100	Harrison and Anderson 1996
Amphibians	7–22	Harrison and Anderson 1996
Reptiles	3–40	Harrison and Anderson 1996
Birds	5–20	Harrison and Anderson 1996
Humans	3	Rice and Baptist 1974

6.1. Arachnidae

6.1.1. Acari

The mean dose to sterilize Acari species ranged from 7.5 to 375 Gy (Table 3). The Chilean false red mite *Brevipalpus chilensis* Baker (Tenuipalpidae), the grain mite *Acarus siro* L. (Acaridae), the brownlegged grain mite *Aleuroglyphus ovatus* (Troupeau) (Acaridae), and the citrus red mite *Panonychus citri* (McGregor) (Tetranychidae) are among the least sensitive species. Hard ticks (Ixodidae), such as *Amblyomma* spp. and *Boophilus* spp., tend to be more sensitive than soft ticks (Argasidae). However, the radiation sensitivity of some tick species appears to change depending on whether the tick is engorged with blood or not (section 4.2.).

6.1.2. Araneae

A recent study (Magris et al. 2015) used the orb web spider *Argiope keyserlingi* (Karsch) (Araneidae) as a model to assess the effectiveness of male sterilization via 40 Gy irradiation and its consequences on male courtship behaviour. The results validated the thread assay and sterilization as legitimate tools for the study of male courtship behaviour and fertilization success. The other known cases of irradiation of spiders for sterilization were conducted to determine the pattern of sperm precedence (Lance and McInnis, this volume) in multiple-mated females. Kaster and Jakob (1997) used a 20-Gy dose to sterilize males of *Holocnemus pluchei* (Scopoli) (Pholcidae), whereas Schneider and Lubin (1996) applied a 150-Gy dose to *Stegodyphus lineatus* (Latreille) (Eresidae). These species showed last-male precedence and complete sperm mixing, respectively.

6.2. Insecta

6.2.1. Coleoptera

The mean sterilization dose for Coleoptera ranged from 43 to over 200 Gy (Table 3). The leaf beetles (chrysomelids) are the most sensitive, followed by coccinellids, scolytids, anobiids, curculionids, and bruchids. Species requiring more than 100 Gy as sterilizing dose are by increasing order: silvanids, tenebrionids, bostrichids, dermestids, laemophloeids, and ptinids. Some data in this order suggested a differential response of males and females towards sterilizing doses of radiation. Males may be more sensitive than females, as in the case of the Japanese beetle *Popillia japonica* Newman (Ladd et al. 1973) and the beetle *Tribolium madens* (Charpentier) (Brower and Tilton 1973), or less sensitive as in the case of the khapra beetle *Trogoderma granarium* Everts (Carney 1959; Nair and Rahalkar 1963).

The effects of gamma radiation on the boll weevil were thoroughly studied with a view to applying the SIT (Earle et al. 1979; Villavaso et al. 1989; Haynes 1993). Males were sterilized by about 80 Gy, but their longevity was poor. The egg-laying capacity of females mated to these males was reduced at doses of 50 Gy or more, but they continued to produce some fertile eggs until doses approached 200 Gy, a dose which rendered the weevils non-competitive (McKibben et al. 2001). Studies were conducted on reducing the negative effects of radiation using improved mass-reared

strains, oxygen-reduced atmospheres, and fractionated radiation doses (Earle et al. 1979; Haynes 1993; McKibben et al. 2001). Even though these effects could be mitigated, the large-scale application of the SIT was not practical and cost-effective, and boll weevil eradication succeeded without the SIT by area-wide integration of pheromone traps, and cultural and chemical controls (McKibben et al. 2001; El-Lissy and Grefenstette 2007).

The detrimental effects of radiation have also been one of the main obstacles in applying the SIT to the sweetpotato weevil *Cylas formicarius* (F.), and in particular the West Indian sweetpotato weevil *Euscepes postfasciatus* (Fairmaire). Digestive obstruction following the collapse of the epithelial tissue of the midgut was suggested as the cause of the short lifespan of gamma-irradiated adults (Sakurai et al. 2000). Nevertheless, mitigation measures, including partial sterility and fractionated-dose irradiation at low temperature, were successful in overcoming these effects (Kumano et al. 2010, 2012), and an AW-IPM programme in Kume Island, Japan, to eradicate these two weevils using the SIT is making good progress (Shimoji and Miyatake 2002; Shimoji and Yamagishi 2004); *C. formicarius* was declared eradicated in 2013 (Haraguchi et al. 2014).

6.2.2. Blattodea

Several Blattodea species have been used in radiobiological studies exploring biochemical, physiological, and genetic properties (Shivaji and Rastogi 1974). In spite of the pest status of many cockroach species, there have been relatively few investigations related to pest suppression using sterile insects, due largely to potential problems with releasing large numbers of males into natural populations (Ross and Cochran 1963; Berndt 1978; Menon 1978; Ross et al. 1981; Gecheva and Apostolova 1986). In terms of sterility and mortality, cockroaches are among the most radiation-sensitive insects, with less than 5 Gy required in some cases (*Blaberus craniifer* Burmeister) to induce sterility (Wharton and Wharton 1959; Ross and Cochran 1963). Sexual differentiation in radiosensitivity was observed in *B. craniifer*, where males were more sensitive than females (Gecheva and Apostolova 1986). In Blattodea, it is the adult stage that is most frequently used for sterilization with ionizing radiation.

6.2.3. Diptera

Radiation sterilization of dipterans generally requires doses from 20 to 160 Gy (Table 3). Drosophilidae and Agromyzidae are among the least radiation-sensitive families of Diptera tested, whereas tachinids are the most sensitive. The late pupal (often pharate adult) stage is preferred for the radiation of most fly species because it is practical to handle and ship pupae, and an acceptable balance between competitiveness and sterility is achieved. In the Culicidae, the late pupal in water, or the early adult stage, is irradiated (Helinski et al. 2006, 2009). Semi-field and field experiments have demonstrated that a radiation dose can be selected that gives sufficient sterility without significantly impacting the competitiveness of male mosquitoes. Furthermore, the ability of radiation-sterilized males to locate and participate in naturally occurring swarms, or to start new swarms, was confirmed in *Anopheles arabiensis* Patton (Ageep et al. 2014). A strategy combining a low radiation dose to ensure female

sterility (SIT), and *Wolbachia*-based IIT (Incompatible Insect Technique), is being developed for *Ae. aegypti* and *Ae. albopictus* to ensure that any unintentionally released *Wolbachia*-infected females would not be able to transmit disease, and also would be sterile, thus avoiding population replacement (Lees et al. 2015).

Tephritidae, the major family in this order that is the target of the SIT, require on average about 85 Gy for sterilization. Tephritids are relatively homogeneous with respect to radiation sensitivity — less than 100 Gy are needed to achieve complete sterility in the five major pest genera (*Anastrepha*, *Bactrocera*, *Ceratitis*, *Zeugodacus*, *Rhagoletis*), and this confirms the generic recommendation of a dose in the range of 100–150 Gy to disinfest agricultural commodities for international trade (Hallman 2000). Many AW-IPM programmes applying the SIT against major pest tephritids have used 100–150 Gy for sterilization, well over the family “average” of 85 Gy. In some early programmes (LaChance et al. 1967), this was a “precaution” to increase the security margin for sterilization, but the overdose often has lowered competitiveness to the point where it reduced the overall ability of irradiated flies to induce sterility into the wild population (Toledo et al. 2004). In recent programmes, these higher doses are usually associated with the use of hypoxia to enhance sterile male competitiveness (section 4.2.) (Fisher 1997).

The Indian tropical midge *Chironomus ramosus* Chaudhuri (Diptera: Chironomidae) tolerated a higher dose of gamma radiation as compared with other known dipterans. The radiation doses required to cause 100% mortality immediately after radiation exposure of egg, larva, pupa and adult stages were 1000 Gy, 3000 Gy, 3200 Gy, and 3500 Gy, respectively (Datkhile et al. 2009). This is one of the least radiation-sensitive species of insects.

6.2.4. Hemiptera

The mean sterilizing dose in the Hemiptera ranged from 55 to 250 Gy (Table 3), with *Circulifer tenellus* (Baker) (Cicadellidae) females being the least sensitive species tested thus far (Amereseckere and Georghiou 1971), and *Halyomorpha halys* (Stål) (Pentatomidae) adults being the most sensitive. In general, adult females required a gamma radiation dose of 50–60 Gy to achieve a high level of sterility. However, higher doses of up to 200 Gy (electrons in this case) were needed to achieve complete sterility in female *Myzus persicae* (Sulzer) (Aphididae) and *Pseudococcus comstocki* (Kuwana) (Pseudococcidae) (Dohino et al. 1997). Adult males typically required a dose between 70 and 200 Gy. For 4th- and 5th-instar nymphs, a lower dose was needed; 75 to 100% sterility was achieved with doses between 5 and 100 Gy. Patterns of relative radiosensitivity between females and males differ among species of Hemiptera (IDIDAS 2018). Considering the male adult stage, the most sensitive bugs are the pentatomids followed by pyrrhocorids, reduviids, and coreids. The least sensitive are cicadellids and mirids.

Only 19 species belonging to 10 out of 53 families of Hemiptera have been subjected to radiation for sterilization. For several species, the feasibility of releasing sterile males for pest suppression was investigated (Shipp et al. 1966; Baldwin and Chant 1971; Tadic 1972; Dyby and Sailer 1999; Calvitti et al. 2000). Some hemipterans are facultatively parthenogenetic, but Steffan and Kloft (1973) argued that, with proper timing and climate, effective genetic control might still be possible.

6.2.5. Hymenoptera

The Hymenoptera include a number of serious pests, such as Africanized honey bees, and various Formicidae (ants) and sawflies. Since bees and ants are social insects with complex life histories, SIT studies have been limited to a few laboratory experiments (Sakamoto and Takahashi 1981). Only data of Apidae and Formicidae species are shown in Table 3. Most experimental irradiations of other hymenopterans (Braconidae, Eulophidae, Pteromalidae), e.g. the parasitic wasp *Habrobracon hebetor* (Say) (Braconidae), have been conducted in conjunction with relatively basic radiobiological, behavioural and physiological investigations (Hoch et al. 2009).

For male honey bees *Apis mellifera* L. (Apidae), the sterilizing dose is 80–100 Gy (Lee 1958). For queens of ants (Formicidae), such as the invasive fire ant *Solenopsis invicta* Buren, the African big-headed ant *Pheidole megacephala* (F.), the little fire ant *Wasmannia auropunctata* (Roger), and the Argentine ant *Linepithema humile* (Mayr), a radiation dose of 150 Gy has been proposed as a phytosanitary treatment (Follett et al. 2016). However, this proposed dose is higher than the dose required to prevent reproduction in the most tolerant ant species tested to date.

6.2.6. Lepidoptera

Lepidopterans as a group are relatively not sensitive to radiation; mean doses for sterilization range from 40 to 500 Gy, with *Thaumetopoea pityocampa* (Denis and Schifferrmüller) (Thaumetopoeidae) requiring the lowest documented average dose of 40 Gy (Baccetti and Zocchi 1962), while three pyralid moths *Plodia interpunctella* (Hübner), *Ephestia eleutella* (Hübner), and *Ephestia calidella* Guénée, the noctuid *Xestia c-nigrum* (L.), the gelechiid *Phthorimaea operculella* (Zeller), the tortricid *Grapholita molesta* (Busck), the crambid *Crocidolomia binotalis* Zeller, and the arctiid *Diacrisia obliqua* Walker (Syn. *Spilosoma obliqua* Walker) required the highest recorded doses (> 400 Gy) for complete sterility of pupae and adults (IDIDAS 2018).

For some moth species, e.g. the coffee leaf miner *Leucoptera coffeella* Guérin-Méneville (Katiyar and Ferrer 1968), even when treated with doses as high as 600 Gy and more, the few male survivors retained some fertility. In contrast to other insect orders, the F₁ progeny of irradiated male lepidopterans are typically more sterile than their parents (inherited sterility). Moreover, the sex ratio in the F₁ generation is biased towards males. Thus, substerilized males can sire completely sterile offspring, and this phenomenon has been exploited in a number of inherited sterility programmes (Marec et al., this volume; Simmons et al., this volume).

6.2.7. Orthoptera

Acrididae (Orthoptera), along with Blaberidae (Blattodea) cited above, are among the most radiosensitive insects known (less than 5 Gy needed for sterilization). This is in agreement with Willard and Cherry (1975) who suggested that large long-lived adults are more radiosensitive than small short-lived adults. However, due to the voracious feeding by nymphs and adults, the release of sterile acridids is not applicable for the control of species such as *S. gregaria*.

6.2.8. *Thysanoptera*

No species of Thysanoptera has been investigated for pest suppression directly using the SIT. However, in Japan, radiation sterilization has been investigated as a quarantine treatment to disinfest cut flowers of thysanopteran pests. Doses up to 400 Gy (electron beam) and 100 Gy (gamma rays) were given to suppress the pests *Frankliniella occidentalis* (Pergande) (EPPO 1994) and *Thrips* spp. (Dohino et al. 1996; Hayasi et al. 1999; Bansiddhi 2000), respectively.

7. CONCLUSIONS

Although radiation is a key component of the SIT, it is generally not given the attention it deserves - in terms of procedures for irradiation, dosimetry, and the choice of an appropriate dose to maximize the induction of sterility in wild females. The development of accurate dose-response curves for the target insect, using precise dosimetry, is a prerequisite of any programme releasing sterile insects. It is important to note here that the focus needs to be on two types of responses: 1) the sterility in the irradiated insect, and 2) the competitiveness for mating. These are opposing responses, and both need to be considered. There are much data for the first kind, but not enough for the second (Rull et al. 2012; Parker, Vreysen et al., this volume). The survey of the available literature presented here shows the wide variation in the response of the different insect species to radiation, and also highlights the need for accurate dosimetry.

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