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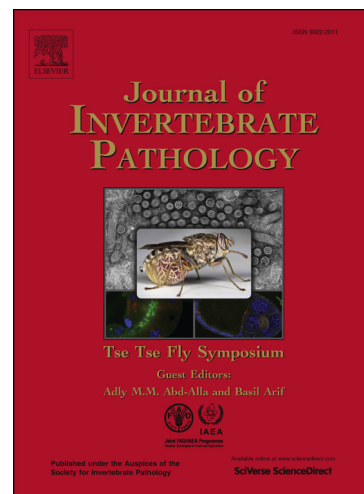
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1 **Insect pathogens as biological control agents: back to the future**

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23 entomopathogenic fungi; entomopathogenic nematodes, *Bacillus thuringiensis*, Bt-crops

24 **Abstract**

25

26 The development and use of entomopathogens as classical, conservation and augmentative
27 biological control agents have included a number of successes and some setbacks in the past 15
28 years. In this forum paper we present current information on development, use and future
29 directions of insect-specific viruses, bacteria, fungi and nematodes as components of integrated
30 pest management strategies for control of arthropod pests of crops, forests, urban habitats, and
31 insects of medical and veterinary importance.

32 Insect pathogenic viruses are a fruitful source of MCAs, particularly for the control of
33 lepidopteran pests. Most research is focused on the baculoviruses, important pathogens of some
34 globally important pests for which control has become difficult due to either pesticide resistance
35 or pressure to reduce pesticide residues. Baculoviruses are accepted as safe, readily mass
36 produced, highly pathogenic and easily formulated and applied control agents. New baculovirus
37 products are appearing in many countries and gaining an increased market share. However, the
38 absence of a practical *in vitro* mass production system, generally higher production costs, limited
39 post application persistence, slow rate of kill and high host specificity currently contribute to
40 restricted use in pest control. Overcoming these limitations are key research areas for which
41 progress could open up use of insect viruses to much larger markets.

42 A small number of entomopathogenic bacteria have been commercially developed for control
43 of insect pests. These include several *Bacillus thuringiensis* sub-species, *Lysinibacillus (Bacillus)*
44 *sphaericus*, *Paenibacillus* spp. and *Serratia entomophila*. *B. thuringiensis* sub-species *kurstaki* is
45 the most widely used for control of pest insects of crops and forests, and *B. thuringiensis* sub-
46 species *israelensis* and *L. sphaericus* are the primary pathogens used for medically important
47 pests including dipteran vectors,. These pathogens combine the advantages of chemical

48 pesticides and microbial control agents (MCAs): they are fast acting, easy to produce at a
49 relatively low cost, easy to formulate, have a long shelf life and allow delivery using
50 conventional application equipment and systemics (i.e. in transgenic plants). Unlike broad
51 spectrum chemical pesticides, *B. thuringiensis* toxins are selective and negative environmental
52 impact is very limited. Of the several commercially produced MCAs, *B. thuringiensis* (*Bt*) has
53 more than 50% of market share. Extensive research, particularly on the molecular mode of action
54 of *Bt* toxins, has been conducted over the past two decades. The *Bt* genes used in insect-resistant
55 transgenic crops belong to the Cry and vegetative insecticidal protein families of toxins. *Bt* has
56 been highly efficacious in pest management of corn and cotton, drastically reducing the amount
57 of broad spectrum chemical insecticides used while being safe for consumers and non-target
58 organisms. Despite successes, the adoption of *Bt* crops has not been without controversy.
59 Although there is a lack of scientific evidence regarding their detrimental effects, this
60 controversy has created the widespread perception in some quarters that *Bt* crops are dangerous
61 for the environment. In addition to discovery of more efficacious isolates and toxins, an increase
62 in the use of *Bt* products and transgenes will rely on innovations in formulation, better delivery
63 systems and ultimately, wider public acceptance of transgenic plants expressing insect-specific
64 *Bt* toxins.

65 Fungi are ubiquitous natural entomopathogens that often cause epizootics in host insects and
66 possess many desirable traits that favor their development as MCAs. Presently, commercialized
67 microbial pesticides based on entomopathogenic fungi largely occupy niche markets. A variety
68 of molecular tools and technologies have recently allowed reclassification of numerous species
69 based on phylogeny, as well as matching anamorphs (asexual forms) and teleomorphs (sexual
70 forms) of several entomopathogenic taxa in the Phylum Ascomycota. Although these fungi have

71 been traditionally regarded exclusively as pathogens of arthropods, recent studies have
72 demonstrated that they occupy a great diversity of ecological niches. Entomopathogenic fungi
73 are now known to be plant endophytes, plant disease antagonists, rhizosphere colonizers, and
74 plant growth promoters. These newly understood attributes provide possibilities to use fungi in
75 multiple roles. In addition to arthropod pest control, some fungal species could simultaneously
76 suppress plant pathogens and plant parasitic nematodes as well as promote plant growth. A
77 greater understanding of fungal ecology is needed to define their roles in nature and evaluate
78 their limitations in biological control. More efficient mass production, formulation and delivery
79 systems must be devised to supply an ever increasing market. More testing under field conditions
80 is required to identify effects of biotic and abiotic factors on efficacy and persistence. Lastly,
81 greater attention must be paid to their use within integrated pest management programs; in
82 particular, strategies that incorporate fungi in combination with arthropod predators and
83 parasitoids need to be defined to ensure compatibility and maximize efficacy.

84 Entomopathogenic nematodes (EPNs) in the genera *Steinernema* and *Heterorhabditis* are
85 potent MCAs. Substantial progress in research and application of EPNs has been made in the
86 past decade. The number of target pests shown to be susceptible to EPNs has continued to
87 increase. Advancements in this regard primarily have been made in soil habitats where EPNs are
88 shielded from environmental extremes, but progress has also been made in use of nematodes in
89 above-ground habitats owing to the development of improved protective formulations. Progress
90 has also resulted from advancements in nematode production technology using both *in vivo* and
91 *in vitro* systems; novel application methods such as distribution of infected host cadavers; and
92 nematode strain improvement via enhancement and stabilization of beneficial traits. Innovative
93 research has also yielded insights into the fundamentals of EPN biology including major

94 advances in genomics, nematode-bacterial symbiont interactions, ecological relationships, and
95 foraging behavior. Additional research is needed to leverage these basic findings toward direct
96 improvements in microbial control.

97

98 1. Introduction

99

100 Since Lacey et al. (2001) addressed the possible future of microbial control of insects, the
101 development of microbial pesticides and implementation of microbial control has included a
102 number of successes and suffered some setbacks. Entomopathogens are utilized in all three
103 categories of biological control, classical, conservation and augmentative, as defined by Hoy
104 (2008a, 2008b) and McCrevy (2008). Some pathogens that are not commercially produced are
105 currently used as classical biological control agents (Huger, 2005; Hajek, 2007; Hajek et al.,
106 2007, 2008, 2009; Hajek and Delalibera, 2010; Bedding, 2008) or conserved as naturally
107 occurring pathogens in agroecosystems (Hummel et al., 2002; Nielsen et al., 2007; Steinkraus,
108 2007b; Pell et al., 2010). Augmentative biological control, using inundatively applied microbial
109 control agents (MCAs), is the most common strategy for employing entomopathogens for control
110 of pest arthropods. Over 50 entomopathogenic viruses, bacteria, fungi, and nematodes are now
111 commercially produced and used augmentatively as microbial pesticides (Figure 1) (Jackson,
112 2003; Goettel et al., 2005; Grewal et al., 2005; Ekesi and Maniania, 2007; Kaya and Lacey,
113 2007; Alves and Lopes, 2008; Copping, 2009; Ravensberg, 2011; Glare et al., 2012; Shapiro-Ilan
114 et al, 2012b; Morales-Ramos et al., 2014). On a global scale, microbial pesticides only account
115 for approximately 1-2% of all pesticides sold (Thakore, 2006; Marrone, 2007; Bailey et al.,
116 2010); however, they have shown long term growth over the past decade in contrast to chemical
117 pesticides, which have consistently declined in the global market (Thakore, 2006; Bailey et al

118 2010). Some sources have recently estimated that the growth in microbial pesticides could reach
119 3% of the pesticide market in 2014 (Glare et al., 2012). A potent driving force for this expansion
120 is the impact of European legislation to restrict residue levels of most synthetic chemical
121 pesticides, and also a forthcoming directive (EC 91/414) to ban many other pesticides including
122 those deemed to be human endocrine disruptors (Ansell, 2008; Bielza et al., 2008; Marx-
123 Stoelting, et al. 2011). These regulations are increasingly requiring farmers growing horticultural
124 produce for sale in the European Union (EU) to drastically reduce use of conventional broad
125 spectrum chemical pesticides. Expansion in biopesticide markets in Europe also reflects the
126 effort of biocontrol scientists to rationalize and simplify the EU microbial pesticide registration
127 procedures as part of the Regulation of Biological Control Agents (REBECA) project, and create
128 a more favorable regulatory system that supports efforts of companies to commercialize MCAs
129 (Ehlers, 2007). The global adoption of harmonized and simpler registration protocols would be a
130 valuable step to promote wider MCA commercial availability (Ehlers 2007; Cherry and Gwynn,
131 2007; Bailey et al., 2010; Kabaluk et al., 2010; Meeussen, 2012; Thornström, 2012). The impact
132 of the growing organic sector in horticulture has also played a role in increasing market
133 opportunities for biopesticides (Rohner-Thielen, 2005). Of the several commercially produced
134 MCAs, *Bacillus thuringiensis* has the majority of market share (Glare et al., 2012) (Figure 1).

135 Entomopathogens are ready made for use in integrated pest management programs and
136 sustainable agriculture (Berger et al., 2007; Pell, 2007; Alves et al., 2008; Lacey and Shapiro-
137 Ilan, 2008; Birch et al., 2011; Glare et al., 2012). They are safe for applicators, the food supply
138 and environment (Lacey and Siegel, 2000; OECD, 2002; Akhurst and Smith, 2002; Hokkanen
139 and Hajek, 2003; Lacey and Merritt, 2003; Hajek and Goettel, 2007; O'Callaghan and
140 Brownbridge, 2009; Mudgal et al., 2013), and their specificity minimizes impacts on beneficial

141 and other non-target organisms. This in turn promotes biodiversity and natural control of pest
142 arthropods by parasites and predators. In the following sections we present information on the
143 current status of entomopathogens as MCAs and prospects for their use in the near and distant
144 future. Some of the key questions that we propose to address are: What are the major advances in
145 microbial control that have been made since 2001? How do we expect biological control to
146 change in the next decade or and in the more distant future? What are the major research or
147 implementation barriers that must be overcome to significantly expand the use of MCAs? What
148 are the societal factors that may hinder or promote their use in the near and distant future?

149

150 **2. Entomopathogenic viruses**

151 *2.1 Major advances since 2001*

152 The role of entomopathogenic viruses in global crop protection has grown in the last decade,
153 although steadily and evolutionarily rather than through any major technical advance. Most new
154 virus products are based on species that have been known and studied for at least two decades
155 and represent commercialization based on extant knowledge rather than recent research efforts.
156 Insect viruses appear to be moving out of narrow “niche” biological control products into the
157 mainstream of commercial farming, reflected in the increased availability of commercial viral
158 pesticides over the last few years. Among the different groups of entomopathogenic viruses
159 (Miller and Ball, 1998; Eberle et al., 2012), most product development and research continues to
160 be focused on the Baculoviridae (BV) (Miller, 1997; Moscardi et al., 2011). Of the four genera
161 of baculoviruses, Alpha-, Beta-, Gamma-, and Deltabaculoviruses (Jehle et al., 2006; Eberle et
162 al., 2012; Herniou et al., 2012), only the lepidopteran-specific nucleopolyhedroviruses (NPV;

163 Alphabaculovirus spp.) and granuloviruses (GV; Betabaculovirus spp.) have been commercially
164 developed to any significant extent (Table 1).

165 Research on developing non-BV viruses for crop protection has continued but only to a
166 limited extent. Studies include fieldwork on the use of tetraviruses for control of heliothines in
167 Australia (Christian et al., 2005) and *Cypovirus* spp. (Reoviridae) (Belloncik and Mori, 1998) for
168 control of oil palm pests in South America (Zeddarn et al., 2003a), though none appear to be
169 close to commercialization. The use of *Oryctes* virus (Nudiviridae) for control of rhinoceros
170 beetle on oil palm in Asia is an ongoing program (Ramle et al., 2005) that has evolved to include
171 the use of a pheromone to collect adults that are then infected and used to disseminate the virus
172 (Jackson et al., 2005). This is an interesting application of the “lure and infect” approach,
173 although as yet there are no definitive published data on the success of this research and efficacy
174 in the field.

175 The dearth of research efforts on these non-BV groups is a significant barrier to further
176 development as crop protection agents, which is surprising in some ways given the importance of
177 some of the potential target pests. Without necessary progress in the fundamental knowledge of
178 viral taxonomy, pathology, ecology and the development of commercially viable mass
179 production systems, non-BV viruses are unlikely to be attractive targets for commercialization
180 by industry in the next decade.

181 The focus on BV for commercialization can be ascribed to several favorable factors. There is
182 more basic knowledge about BV biology, pathology and ecology than for any other group of
183 invertebrate viruses, and the wealth of data greatly facilitates product development and
184 registration. In addition, there are many scientists with the necessary knowledge to support
185 commercialization initiatives, and established centers of BV research are more geographically

186 widespread, enabling collaborations between academics and local microbial pesticide companies.
187 High levels of *in vivo* replication of most BV that are of commercial interest is also a key factor
188 in making commercial production potentially economically feasible.

189 The infective stage of BVs is characterized by circular double stranded DNA within rod
190 shaped nucleocapsids that are encased within occlusion bodies (OB) formed of crystalline
191 protein. The details of BV life history, biology and ecology are covered in detail elsewhere and
192 are not discussed here (see Miller, 1997; Fuxa, 2004; Cory and Myers, 2003; Cory and Evans,
193 2007; Moscardi et al., 2011; Harrison and Hoover, 2012). The robust nature of the OB is a factor
194 facilitating commercial baculovirus product development as it is readily amenable to
195 formulation, application and long-term storage than non-occluded insect viruses. OBs can be
196 visualized using phase contrast light microscopy, facilitating quantification of BV without the
197 need for electron microscopy, which requires expensive equipment that often is not readily
198 available to microbial pesticide companies. In the last decade, there has been a significant
199 expansion in range of commercial BV products (Kabaluk et al., 2010; Gwynn 2014), notably in
200 the range of BV insecticides available in Europe and North America. Elsewhere the picture is
201 mixed with significant expansion in the production and use of BV microbial pesticides in parts of
202 Asia, Australasia and South America, but as yet little expansion of use in Africa (Cherry and
203 Gwynn, 2007; Kabaluk et al. 2010; Moscardi et al., 2011).

204 The focus on BV is in large part due to the importance of these pathogens in controlling
205 some globally important lepidopteran pest species such as *Helicoverpa* spp. (Rowley et al. 2011)
206 and *Spodoptera* spp. (Table 1). These pest species have a marked propensity to rapidly develop
207 resistance to conventional chemical insecticides, making their control challenging. These species
208 also are pests on a wide range of crops, providing potential market niches for BV in field crops

209 and in protected crops grown in polytunnels and glasshouses (Grzywacz et al., 2005; Arrizubieta
210 et al., 2014). In China, NPV supply has expanded with nine BV products now commercially
211 available. There are at least 12 Chinese manufacturers of *Helicoverpa armigera* NPV
212 (HearNPV) and several of *Spodoptera litura* NPV (SpltNPV), *Autographa californica* NPV
213 (AucaMNPV), *Plutella xylostella* GV (PlxyGV) and *Spodoptera exigua* NPV (SeMNPV) as well
214 as a number of other BV products (Sun and Peng, 2007; Yang et al., 2012). It is difficult,
215 however, to determine the total use of BV in China. One source estimated that in 2007 around
216 250 tonnes of formulated material was produced, 80% of which was HearNPV, used on up to
217 100,000 ha (Sun and Peng, 2007). A more recently published estimate stated that up to 2,000
218 tonnes of formulated BV products may be produced annually, from which it may be inferred that
219 areas treated have expanded significantly from the earlier estimate, and may have reached up to 1
220 million ha (Yang et al., 2012). In India, many new suppliers of HearNPV and SpltNPV have
221 appeared in recent years following the adoption of simplified microbial pesticide registration and
222 in response to the growing problem of synthetic insecticide resistance (Department of
223 Biotechnology India, 2007; Rabindra and Grzywacz, 2010). The total production of BV in India
224 was estimated to be in excess of 50 tonnes in 2004 (Singhal, 2004) with both public and private
225 sector organizations active in manufacturing. Quality control issues remain a concern in India
226 and parts of Southeast Asia (Jenkins and Grzywacz 2000; Kambrekar et al., 2007; Grzywacz et
227 al. 2014a). It remains to be seen if truly large-scale market penetration can be achieved in these
228 regions with the existing generation of products. Australian growers have incorporated BV for
229 management of *H. armigera* in field crops, and importation of *Helicoverpa zea* NPV
230 (HezeSNPV) for *H. armigera* control is now supplemented by local sources of a HearSNPV
231 isolate (Buerger et al., 2007; Hauxwell et al., 2010). A major breakthrough in adoption of BV by

232 producers was bringing together new midge resistant sorghum hybrids with HearSNPV to
233 produce an IPM system that controlled the two major crop pests alongside local production of
234 the BV (Franzmann et al., 2008). HearNPV, SpltNPV and SeMNPV are registered in Thailand
235 and Vietnam, though supply currently appears to depend on imports and public sector suppliers
236 rather than local commercial sources (Nakai and Cuc, 2005; Ratanastien et al., 2005; Skovmand,
237 2007). In South America, Brazil leads BV development with a well-established program for
238 production and use of *Anticarsia gemmatalis* NPV (AngeMNPV) for control of velvet bean
239 caterpillar on soy (Moscardi, 1999; 2007; Sosa-Gómez et al., 2008). More recently, production
240 and use of AngeMNPV has begun in Mexico (Williams et al., 2013a). The production of
241 AngeMNPV was initiated in Brazil as a public sector project but commercial producers
242 subsequently were brought in to scale up production. Mass-reared insect production was later
243 introduced in Brazil to supplement the original field-based production system when the treatment
244 areas rose to 2 million ha in 2004 (Moscardi, 2007). However, since the use of no-tillage systems
245 involving the routine prophylactic use of broad spectrum insecticides in place of BV applications
246 have been widely adopted, AngeMNPV is now used on less than 300,000 ha (Moscardi et al.,
247 2011; Panazzi, 2013). The rapid shift in the fortunes of what was a very successful microbial
248 pesticide is an illustration of the dynamic nature of modern commercial agriculture and how
249 continued user acceptance of successful microbial pesticides cannot be taken for granted.
250 Despite the decrease in use, this program remains a model for public sector development of a BV
251 that successfully spawned large-scale commercial use. Development of *Spodoptera frugiperda*
252 NPV (SpfrMNPV) for controlling *S. frugiperda* in maize, *Condylorrhiza vestigialis* NPV
253 (CoveNPV) for pest control on poplar trees (*Populus* spp.) and *Erinnyis ello* GV for cassava pest
254 control (Bellotti et al., 1999; Moscardi et al., 2011) is also underway by research institutes in

255 Brazil, while commercial production of SpfrMNPV and *Autographa californica* MNPV
256 (AcMNPV or AucaMNPV) is also reported in Guatemala, although the scale of use is not clear
257 (Sosa-Gómez et al., 2008). Efforts continue to extend the use of the successful potato tuber moth
258 *Phthorimaea operculella* GV (PhopGV), currently produced in Bolivia by the public or non-
259 government organization (NGO) sector (Sporleder, 2003; Kroschel and Lacey, 2008; Sporleder
260 and Kroschel, 2008; Lacey and Kroschel, 2009) for both field crop (Wraight et al., 2007b;
261 Arthurs et al., 2008c; Sporleder and Kroschel, 2008; Sporleder and Lacey, 2013) and stored
262 product use in North and South America (Arthurs et al., 2008b, Sporleder and Kroschel, 2008;
263 Lacey et al., 2010a; Sporleder and Lacey, 2013). Studies have also focused on the formulation of
264 PhopGV (Sporleder, 2003; Arthurs et al., 2008b) and its propagation *in vivo* (Sporleder et al.,
265 2008) for control of the pest host. In some areas of South America, a new potato pest, *Tecia*
266 *solanovora*, has supplanted *P.operculella* as the main potato pest, threatening the efficacy of
267 PhopGV in potato stores. The identification of a new strain of PhopGV showing activity against
268 both pests is particularly promising; without such dual activity, farmer use is likely to decline
269 precipitously as *T. solanovora* spreads (Gómez-Bonilla et al., 2011).

270 One of the most widely used commercially developed viruses is the codling moth, *Cydia*
271 *pomonella* granulovirus (CpGV). Although CpGV was developed and commercialized for use in
272 Europe in 1987 (Hüber, 1998; Cross et al., 1999; Vincent et al., 2007), it was registered in North
273 America more recently (Vincent et al., 2007; Lacey et al., 2008b) and is now used worldwide
274 (Lacey et al., 2008b; Sosa-Gómez et al., 2008). A comprehensive review of the CpGV literature
275 by Lacey et al. (2008b) concluded that CpGV provides good codling moth population control.
276 Other reasons for its widespread adoption are that no spray interval is required throughout the
277 growing season and before harvest, and it is safe for applicators, the food supply and non-target

278 organisms. Although it is widely used in Europe and in North America, adoption by conventional
279 growers is still limited compared to organic growers. The principal caveat for its use is the
280 relatively low persistence of the virus due to solar degradation, necessitating frequent re-
281 application when codling moth pressure is high. Indeed, given the issue of its low persistence in
282 the field, its relatively successful use by the apple industry is an interesting illustration that even
283 products with less than optimal performance can succeed under the right circumstances. It may
284 well be that if application can be timed to coincide with peak fruit entry by first instar codling
285 moth larvae and the BV can rapidly infect a high proportion of larvae before significant damage
286 occurs, adequate control can be achieved even in a context where the BV has low persistence
287 (Cherry, 2000; Grzywacz et al., 2008). Another factor in CpGV's favor is high virulence and the
288 ease and speed with which it infects (Ballard et al., 2010a). Pest ecology may be another
289 element; in many apple growing systems there are only one or two pest generations per year and
290 growers can target the early larval stages with a high degree of confidence, ensuring that even a
291 short lived virus can achieve acceptable control (Lacey and Shapiro-Ilan, 2008). It must also be
292 noted that CpGV is not a stand-alone product in apple production but a component in a well-
293 developed "soft" IPM system (Lacey et al., 2008b). BVs like other biological control agents
294 (BCA) may perform best as part of a comprehensive IPM system rather than as chemical
295 substitutes (Lacey and Shapiro, 2008). The success of soft IPM in apples also may be related to
296 the long duration of tree crop systems that facilitate the successful establishment of natural
297 enemy complexes, a situation less common in annual crops. Another issue may be that the
298 relatively high profile and consumer demand for "organic apples" provides an additional market
299 incentive to enable biological insecticides such as CpGV to capture a significant market niche.

300 Expansion of BV use is not without potential problems. Following widespread adoption of
301 CpGV in parts of Europe, extremely high levels of resistance have been reported in certain
302 locations where it has been used for 20 years or more (Fritsch et al., 2005; Eberle and Jehle,
303 2006; Sauphanor et al., 2006; Zichová et al., 2013). Laboratory studies reveal that rapid
304 development of extreme resistance (100,000 resistance ratio) is possible due to sex-linked
305 inheritance of a dominant resistance gene (Asser-Kaiser et al., 2007) and involves a specific
306 mutation affecting an early block on virus replication (Asser-Kaiser et al., 2011). It has been
307 shown that this resistance can be overcome by using BV products containing different CpGV
308 isolates than the original Mexican strain used in all earlier CpGV products (Eberle et al., 2008),
309 and a number of new products incorporating the new CpGV isolates have now been brought to
310 market (Zichová et al., 2013; Andermatt Biocontrol, 2014). However, to ensure future
311 sustainability, an integrated approach that alternates other soft interventions with CpGV products
312 is recommended when the virus is used extensively within a region (Lacey et al., 2008b). An
313 interesting contrast with *C. pomonella* resistance is use of AngeMNPV in Brazil. Despite the
314 ease with which resistance to AngeMNPV can be selected for in laboratory populations of *A.*
315 *gemmatalis* (Abot et al., 1997) and the extensive use of AngeMNPV over many years, no reports
316 of field resistance to AngeMNPV have been confirmed (Moscardi, 2007). This contrast may
317 indicate that widespread geographical use of a virus is less a factor in selecting resistance than
318 reliance on a single genetic strain. If so, producers of BV products should plan to incorporate
319 either a wild type mixture of strains in a product or have alternate strains developed and available
320 as part of a product resistance management strategy.

321 The appearance of a commercial GV product against false codling moth, *Cryptophlebia*
322 *leucotreta*, in South Africa is an important step as the first commercially available BV produced

323 in Sub-Saharan Africa (Singh et al., 2003; Moore et al., 2004a). Another BV that has been under
324 active development in Africa is the NPV of *Spodoptera exempta* NPV (SpexNPV) for control of
325 the African armyworm, a major migrant pest in Africa (Grzywacz et al., 2008). A pilot
326 production plant was set up in Kenya by a private commercial producer (Van Beek, 2007) and a
327 HearNPV product from this producer was registered in Kenya and Ghana in 2012; however, the
328 scale of use is unclear. Diamond back moth, *Plutella xylostella*, is another global pest that has
329 been a priority target for research of both *P. xylostella* GV (PlxyGV) and *P. xylostella* NPV
330 (PlxyMNPV) (Kariuki and Macintosh, 1999; Grzywacz et al., 2004). A comparison of PlxyGV
331 and PlxyMNPV showed that both had similar pathogenicity on the basis of OB counts but that
332 PlxyGV infections produced many more OBs per unit of host weight (Farrar et al., 2007).
333 Commercial PlxyGV products are available in China though the scale of use is uncertain (Yang,
334 2012).

335 Turfgrass pest control has also been a focus for pests such as *Agrotis ipsilon* using an NPV
336 (AgipMNPV, Prater et al., 2006). Much of the work involves protecting golf course turf, but
337 while AgipMNPV can give good control of early instars, its persistence is limited by frequent
338 mowing. Additionally, exposure to UV reduces secondary cycling of the virus (Bixby-Brosi and
339 Potter, 2010). BV isolates under development by the public sector (Table 1) have not yet
340 attained product status.

341 Research on expanding use of other existing BV products continues, including the use of
342 *Spodoptera exigua* NPV (SeMNPV) in glasshouses in southern Europe (Lasa et al., 2007). An
343 interesting development is the commercialization in Japan of a joint formulation of *Adoxophyes*
344 *orana* GV and *Homona magnanima* GV for controlling two tortrix pests of tea (Kunimi, 2007).

345 The use of BV in forest insect pest control in North America and Europe, a traditional focus
346 of BV research (Cunningham, 1995; Martignoni, 1999; Podgewaite, 1999), has remained limited.
347 The development of some forest pest BV, such as the gypsy moth NPV has continued (Cadogan
348 et al., 2004; Moreau and Lucarotti, 2007) and commercial production of sawfly *Neodiprion*
349 *abietis* is now also underway (Lucarotti et al., 2007). The lack of expansion of BV use in forest
350 pest control may reflect the preferential adoption of *Bacillus thuringiensis*-based products, with
351 their ready availability and wider host range (Moreau and Lucarotti, 2007; van Frankenhuyzen et
352 al., 2007), rather than rejection of BV microbial pesticides. In Asia a number of forest pest BV
353 are either in production or use in China, Japan and India; the scale of use remains unclear,
354 although probably limited (Nair et al., 1996; Peng et al., 2000; Kunimi, 2007; Sun and Peng,
355 2007; Yang et al., 2012). Use of BV in stored products has also been a focus of research,
356 particularly on *Plodia interpunctella* GV (PlinGV) (Vail et al., 1991, 1993). PlinGV has shown
357 promise for control both through direct action and auto-dissemination but as yet has not been
358 commercially developed.

359

360 **2.2 Research issues that constrain expansion of the use insect viruses**

361 Mass production of BV at a cost most potential users can bear remains a significant issue.
362 Production of commercial BV insecticides is still dependent on *in vivo* systems utilizing
363 specially reared or wild collected insects (Reid et al., 2014; Grzywacz et al., 2014b). *In vivo*
364 systems for production of BV in live larvae remain the normal production method for
365 commercial companies and for public sector programs (Moscardi, 1999; Van Beek and Davies,
366 2009; Grzywacz et al., 2014a) but the relatively high cost of producing BV in living insects
367 compared to their chemical insecticide counterparts remains a constraint as farm prices are

368 difficult to reduce below \$20 per ha and scaling up *in vivo* BV production with its demands for
369 high quality disease-free insects is also a challenge (Reid et al., 2014). The use of automation
370 and mechanization in inoculation, rearing, and harvesting has facilitated mass production and
371 made BV a viable commercial option for the current range and usage scale. However, this
372 manufacturing approach remains unattractive to many companies in North America and Europe
373 that are unfamiliar with mass insect culture as a mainstream production technique, and while, the
374 *in vivo* production approach remains capable of meeting the current market needs, the ability to
375 produce the amounts of BV needed for large scale field crop protection is far from certain. It
376 remains to be seen if the recent sharp decline in the use of AgMNPV in Brazil after a major
377 investment in laboratory-based mass production facilities (Moscardi et al., 2011; Panazzi, 2013)
378 will have a significant impact on the willingness to fund a major expansion of *in vivo* BV
379 production.

380 While most viral pesticides are produced in specialized facilities, field production *in vivo* has
381 been a viable approach for a few commercial BV products such as AgMNPV in developing
382 countries (Hunter-Fujita et al., 1998; Moscardi, 2007; Alves and Lopes, 2008). Field production
383 is planned for SpexNPV in Africa (Grzywacz et al., 2014b), although large scale commercial
384 viable mass production has yet to be successfully established for any BV other than AgMNPV.

385 Facing future needs for large-scale mass production of BV, *in vitro* cell culture remains a
386 major approach to overcoming supply and cost constraints that limit BV use (Black et al., 1997,
387 Moscardi et al., 2011). Mass production of hosts to produce viruses has been under development
388 for 30 years but has not yet been successfully scaled up to the levels required to meet
389 commercial acceptability (Granados et al., 2007). While many cell lines capable of supporting
390 BV replication exist, the cells are relatively fragile compared to the bacterial and yeast cells

391 normally used in large scale cell culture systems. Meeting commercial needs for BV production
392 would require bioreactors of >10,000 l that are capable of continuous high efficiency production.
393 (Black et al., 1997, Reid et al., 2014). Successful insect cell production has been reported in a
394 number of different bioreactors but only at volumes of 20- 600 l (Reid et al 2014). Besides
395 developing large-scale reactors suitable for insect cell lines, *in vitro* systems require low cost
396 chemically defined media optimised for insect cell production to be cost effective and this is also
397 not yet available. BV production quality also has been an issue; in particular, low cell yield and
398 the maintenance of acceptable phenotypic qualities are constraints yet to be overcome (Pedrini et
399 al., 2006; Nguyen et al., 2011). Thus, while research to develop cost effective *in vitro* systems
400 continues (Granados et al., 2007; Szewczyk et al., 2006; Moscardi et al., 2011), there are as yet
401 no indications that commercial production will begin in the near future, though technical and
402 commercial “road maps” for such a ventures have been developed (Reid et al., 2014).

403 The slower killing speed of BV compared with most synthetic insecticides remains a
404 significant barrier to their wider adoption (Copping and Menn, 2000; Szewczyk et al., 2006).
405 Speed of action remains an important factor in selecting strains because faster acting strains
406 would reduce crop damage and would be more attractive to users accustomed to the rapid kills
407 obtained with many, though not all, chemical pesticides. A major focus of applied research to
408 increase speed of action has been genetic modification (GM) of BV to insert or delete genes that
409 quickly initiate cessation of feeding and accelerate death. The inserted genes include insect
410 specific toxins from the scorpions *Androctonus australis* and *Leiurus quinquestriatus*, the spider
411 *Tengeneria agrestis*, the itch mite *Pyemotes tritici* and juvenile hormone esterases (Burdan et al.,
412 2000; Bonning et al., 2002; Szewczyk et al., 2006). Despite promising field trial results,
413 commercial development of these GM BVs appears to have stalled, perhaps because the

414 recombinants produce poor yields in current *in vivo* systems or because the climate of public
415 opinion and regulatory barriers are not sufficiently favorable to GM products in major potential
416 markets such as the EU (Black et al., 1997; Glare et al., 2012).

417 The adoption of new natural mutant virus strains such as non-liquefying SfMNPV (Valicente
418 et al., 2008) is another route for improving the cost effectiveness of BV that would not face such
419 perceptual or registration barriers; however, the use of a natural faster-acting strain in practice
420 may not be without drawbacks. A faster killing strain of *S. frugiperda* NPV (SpfrMNPV) was
421 identified, but it was found to produce fewer OBs than the slower killing isolate, an evolutionary
422 trade-off that is probably common and could reduce the impact of secondary cycling (Behle and
423 Popham, 2012). Thus, despite extensive research in genetic modification to overcome some of
424 the recognized BV constraints of restricted host range, slower action, and sensitivity to UV, no
425 BV recombinant products with improved performance have been marketed nor do they seem
426 likely to be in the near future. This is partly due to the technical failure to develop recombinants
427 with the desired characteristics but may also reflect the rising costs of registering and deploying
428 GM technology. In addition, recently published research on the genetic and genomic aspects of
429 BV (with 43 genomes sequenced) has thrown an interesting light on BV relationships and
430 evolution (Jehle et al., 2006; Eberle et al., 2009; Herniou et al., 2012).

431 It has been hoped that genomic data would assist the development of products with improved
432 efficacy, host range, etc. (Inceoglu et al., 2006), but as yet there has been no commercial impact.
433 While generally OBs are stable, they are sensitive to UV inactivation as well as phytochemical
434 degradation on some plant species (Cory and Hoover, 2006; Cory and Evans, 2007; Behle and
435 Birthisel, 2014). Specific phytochemical mechanisms that interfere with BV infectivity on crops
436 have been identified in cotton (Hoover et al., 1998; Hoover et al., 2000) and, more recently, in

437 chickpea (Stevenson et al., 2010). The low persistence of BV on these and other crops is still
438 perceived as a real limitation to the current generation of BV microbial pesticides (Copping and
439 Menn, 2000; Moscardi et al., 2011; Behle and Birthisel, 2014). However, given the relative
440 commercial success of CpGV, which has a short persistence time due mainly to solar
441 inactivation, limited persistence may not be an insurmountable barrier to adoption provided
442 products give a degree of control that meets the users core requirements.

443 BV can be applied using any commercial spraying system without special formulation (Gan-
444 Mor and Mathews, 2003), although stickers, gustatory stimulants and UV protectants are often
445 routinely incorporated into tank mixes to improve efficacy (Burges and Jones, 1998; Behle and
446 Birthisel 2014). Effective application rates for field use of NPV species that contain multiple
447 virions vary between $0.5-5 \times 10^{12}$ OBs per ha (Moscardi, 1999), while for the GV with only one
448 virion per occlusion body, rates can be higher (Moscardi, 1999). Research into new technology
449 for applying BV seems to have advanced little in recent years, perhaps in recognition that
450 farmers' decisions on the acquisition and use of sprayers is not likely to be driven to any
451 significant extent by their specific ability to deliver microbial agents such as BV. There is now
452 more interest in using precision application technologies for crop protection. In the next decade,
453 use of minimal or precisely applied inocula in place of the traditional blanket spraying may be
454 one of the most interesting avenues for exploiting BV more successfully and overcoming issues
455 of cost and availability.

456 In addition to improving speed of kill, efficacy, host range, and persistence, applied research
457 on formulation of BV remains one of the most important routes to BV product improvement
458 (Burges and Jones, 1998; Behle and Birthisel, 2014). However, published research on this issue
459 is very limited, probably due to proprietary issues, so it is unclear if limited publications reflect

460 lack of significant progress. A number of improvements have been reported but it is not clear if
461 advances are likely to appear in products in the near future. Most virus products are produced
462 and sold as suspension concentrates, wettable powders and granules.

463 A minimum shelf life of 18 months was recommended over 30 years ago (Couch and
464 Ignoffo, 1981) and some products are now available that meet this standard (Burges and Jones,
465 1998; Lacey et al., 2008b); these usually include adjuvants that stabilize the virus and improve
466 suspension in water. Factors that affect shelf life of viruses (temperature and formulation
467 components) have been reported for the NPV of the celery looper *Anagrapha falcifera*
468 (AnfaMNPV) (Tamez-Guerra et al., 2000; Behle et al., 2003) and CpGV (Lacey et al., 2008a).

469 Some producers ship virus as frozen product and advise keeping the virus frozen until used,
470 although this may not always be possible under operational conditions. Freezing is not essential
471 to preserve BV, which can remain active in purified suspensions over long periods, even at room
472 temperature. However, refrigeration or freezing does appear to be necessary to prevent the loss
473 of activity related to the proliferation of contaminant bacteria and the oxidation of host derived
474 lipids (Burges and Jones, 1998) and, thus, maintain the infectivity of mass produced suspensions
475 (Lasa et al., 2008). The need for cold storage of BV is less of constraint in glasshouse and
476 protected crops where use of biological control agents such as predators and parasitoids,
477 requiring special storage or immediate use on receipt, has become increasingly common. It does,
478 however, limit adoption in many field crops where biological control agents are less widely
479 utilized.

480 The wider availability of formulations with ambient shelf life comparable to synthetic
481 pesticides (> 2 years) would be a substantial stimulus for expansion of BV use. Air-dried, spray-
482 dried, and freeze-dried formulations have been widely studied with promising results for storage

483 stability and activity (Alcázar et al., 1992; Tamez-Guerra et al., 2000, 2002; McGuire et al.,
484 2001; Behle et al., 2003; Arthurs et al., 2008b). Spray drying of AnfaMNPV did not significantly
485 reduce activity of lignin formulations over 6 months storage at 4°C (Behle et al., 2003). Freeze
486 dried formulations of the PhopGV were comparable in activity to emersion in an aqueous virus
487 suspension (Arthurs et al., 2008b). Freeze dried and microencapsulated formulations of
488 HearSNPV were also found to be as effective in the field as aqueous suspensions when applied
489 on chickpea (Cherry et al., 2000). However, AnfaMNPV spray-dried formulations were reported
490 to have higher residual activity compared with a commercial glycerin-based formulation (Behle
491 et al., 2003). Differences in results may relate to specific crop-pest factors such as chemical
492 inactivation reported on chickpea, so formulations may need to be tailored in some cases to the
493 specific crop (Stevenson et al., 2010). Encapsulation of viral OBs in lignin via spray drying has
494 been developed and tested with MNPV and GV and produced higher mortality and longer
495 persistence than unformulated controls (Tamez-Guerra et al., 2000; McGuire et al., 2001; Behle
496 et al., 2003; Arthurs et al., 2006; 2008a, Behle and Popham 2012). Castillejos et al. (2002)
497 reported considerably greater persistence with a granular phagostimulant formulation of the
498 SfMNPV than with an aqueous suspension. In contrast, the commercially produced particle films
499 and waxes, marketed as sunburn protectants for fruit are reported as providing no significant
500 additional protection for CpGV (Lacey et al., 2004; Arthurs et al., 2006; 2008a).

501 A principal concern of growers is the need for frequent reapplication of BV due to rapid
502 inactivation when exposed to sunlight (Behle and Birthisel, 2014). BV are especially sensitive to
503 the ultraviolet spectrum (Ignoffo, 1992; Burges and Jones, 1998; Tamez-Guerra et al., 2000;
504 Lacey and Arthurs, 2005), although specific host plant phytochemical factors can also contribute
505 to low persistence on some crops and tree species (Cory and Hoover, 2006). The relative role of

506 low UV persistence in constraining BV product use varies significantly due to a complex of
507 biotic and abiotic crop specific factors such as UV levels, crop architecture, pest infestation
508 patterns and cropping practices (Stevenson et al., 2010). In tropical crops exposed to high UV,
509 persistence of BV can be less than 24 hours; but persistence of other microbial pesticides such as
510 Bt and even chemicals can also be short on these crops due to the combination of high UV and
511 high temperature, which drives inactivation, chemical breakdown and volatilization (Cherry et al.,
512 2000).

513 One issue complicating the evaluation of research on UV persistence is the variability of
514 experimental protocols used by different researchers. Some researchers evaluate natural sunlight
515 exposure, which also has issues of variability, but many studies use various artificial UV sources
516 that may not closely mimic natural sunlight spectra or leaf surface exposure. Exposure distances
517 and duration vary and the choice of substrate can be a confounding issue. For example, direct
518 heating effects may confound the effect of UV exposure when substrate temperatures are not
519 restrained within environmentally valid bounds. Optical brighteners (Tinopal, Blankophor P167,
520 and other stilbene derivatives), with and without titanium dioxide, have been shown to increase
521 the persistence of NPV and GV (Farrar et al., 2003; Monobrullah and Nagata, 2001; Sporleder,
522 2003). However, Sajap et al. (2009) found that, although adjuvants such as Tinopal gave
523 significantly improved UV protection in laboratory studies of SpltMNPV, in subsequent field
524 trials on brassicas, no clear advantage was conferred over unformulated SpltNPV. A number of
525 other materials that absorb specific wavelengths, including specialized dyes, chemicals and
526 natural substances such as lignin sulfate, polystyrene latex, Congo Red, green tea, antioxidants,
527 iron oxide and others have been tested to improve the residual activity of entomopathogenic
528 viruses (Burgess and Jones, 1998; Charmillot et al., 1998; Ballard et al., 2000b; de Morães Lessa

529 and Medugno, 2001; McGuire et al., 2001; Sporleder, 2003; Asano, 2005; Arthurs et al., 2006;
530 Shapiro et al., 2008). Molasses, sucrose and skimmed milk powder have also been reported to
531 slightly improve persistence of CpGV (Charmillot et al., 1998; Ballard et al., 2000b). Alves et al.
532 (2001) demonstrated greater persistence of NPV in an oil emulsion formulation than in a
533 wettable powder for control of *A. gemmatalis*. UV protected petroleum spray oils were also
534 found to be effective with HearSNPV (Mensah et al., 2005). In considering formulations that
535 improve UV stability, it is not only performance that should be taken into account. Some
536 experimentally demonstrated formulation additives have not been adopted for commercial use
537 due to factors such as high cost, phytotoxicity, storage incompatibility, cosmetic unacceptability
538 on fresh produce, or because application at the required concentrations, is impractical due to high
539 viscosity or blocking of spray filters as occurs with some particulate additives.

540 It has been suggested that the success of HearNPV in Australia is related to very rapid
541 acquisition, mitigating the problem of low BV persistence on crops (Murray et al., 2001),
542 although the use of additives in tank mixes to improve efficacy of HearNPV is also an important
543 factor in its success (Mensah et al., 2005; Hauxwell and Reeson, 2008). Increasing the
544 attractiveness of spray deposits by adding attractants and feeding stimulants to tank mixes has
545 shown promise in accelerating the acquisition of virus; for example, molasses is reported to be
546 one of the most effective feeding stimulants for codling moth larvae (Ballard et al., 2000b).
547 Other phagostimulants with potential for improving efficacy of CpGV include monosodium
548 glutamate (Pszczolkowski et al., 2002) and trans-1-aminocyclobutane-1,3-dicarboxylic acid
549 (trans-ACBD) (Pszczolkowski and Brown, 2004). However, use of high concentrations of
550 additives such as molasses may have unacceptable side effects such as stimulating disfiguring
551 fungal growth such as sooty mold on fresh produce. Schmidt et al. (2008) reported significant

552 improvement of CpGV used in conjunction with the pear ester larval and adult attractant
553 kairomone. However, Arthurs et al. (2007) reported inconsistent results in similar tests on apple
554 and pear, and suggested that more practical improvements in formulation and application
555 strategies were needed. Knight and Witzgall (2013) reported significant increases in larval
556 mortality when combining any one of three yeasts, *Metschnikowia pulcherrima*, *Cryptococcus*
557 *tephrensis* or *Aureobasidium pullulans*, with CpGV compared with CpGV alone. A field trial
558 confirmed that fruit injury and larval survival were significantly reduced when apple trees were
559 sprayed with CpGV, *M. pulcherrima* and sugar.

560 Wetting and sticking surfactants are generally recommended to improve mixing, reduce
561 surface tension and increase deposition over plant surfaces (Burgess and Jones, 1998). The use of
562 additional stickers with entomopathogenic viruses was reported by Ballard et al. (2000), Tamez-
563 Guerra et al. (2000) and Arthurs et al. (2008a). Optical brighteners have also been shown to
564 enhance the infectivity of a number of NPV species, a response related to effects on the
565 peritrophic membrane (Morales et al., 2001; Murillo et al., 2003; Martinez et al., 2004; Farrar et
566 al. 2005; Toprak et al., 2007). Similarly, Cisneros (2002) demonstrated a synergistic effect of 1%
567 borax on activity of SfMNPV. Formulation research has not yet produced significant impacts on
568 the overall performance of commercial BV products, but the availability of formulations with
569 substantially improved persistence would improve product attractiveness for many crop systems.

570 The use of other additives to enhance the efficacy of BV infection has been widely explored.
571 The enhancins are a group of viral proteins recognized to increase both NPV and GV viral
572 potency in heterologous hosts and suggest significant potential to expand the host range of
573 specific BV (Slavicek, 2012), although these have not yet been developed for commercial use.
574 Azadaractin and other neem-derived chemicals also have been reported to effectively reduce the

575 BV dosage needed to control pests in bioassays (Zamora-Aviles et al., 2013), and if validated in
576 the field, could prove useful in lowering the cost of product.

577 The impact of expanded GM crop production on the use of BV remains to be determined.
578 While the adoption of insect resistant GM crops can remove established markets for BV in some
579 crops such as cotton (Buerger et al., 2007), it may also present opportunities for incorporating
580 BV into GM cropping systems to cope with secondary non target pests, or as part of an insect
581 resistance management strategy (Thakore, 2006; Kennedy, 2008). HzNPV significantly
582 improved control of *H. zea* in GM sweet corn, although not as consistently as application of the
583 insecticide spinosad (Farrar et al., 2009). Research on the use of insect virus genes in transgenic
584 plants as a new source of insect resistance may, in the long term, provide the capability to utilize
585 BV in crop protection (Liu et al., 2006).

586 While BV may be deployed using basic strategies of inoculation, conservation or
587 augmentation, in current practice, BV is applied augmentatively as a microbial pesticide on an
588 “as needed” basis. In the opinion of some researchers, however, pesticidal use is a barrier to
589 realising the full potential of biological agents and their ability to replicate, persist and spread
590 (Waage, 1997). An alternative to conventional spray application is dissemination of BV
591 formulations via novel lure and contaminate technologies incorporating pheromones (Vega et al.,
592 2007). Adult insects attracted to BV inoculum become surface contaminated and pass the virus
593 to egg surfaces and subsequently to hatching larvae. This strategy has been recently applied to
594 orchard pests (Cross et al., 2005); other examples are presented by Vega et al. (2007).

595 Despite the recognized importance of secondary cycling via horizontal and vertical
596 transmission of BV in pest populations, there has been little deliberate exploitation of BV
597 capacity to replicate and cycle in the way that specific inoculation strategies are used for *Oryctes*

598 virus (Jackson et al., 2005) or cropping practices designed to promote BV conservation
599 (Moscardi, 1999; Cory and Evans, 2007). Virus ecology remains a very active field of research
600 for both crop and forest pests (Cory and Myers 2003; Fuxa 2004; Harrison and Hoover 2012),
601 expanding our knowledge of BV epidemiology and virus host population dynamics. Studies have
602 included secondary cycling, horizontal and vertical transmission, and the interaction of BV with
603 other pathogens such as *Wolbachia* (Graham et al., 2010) and offer interesting insights into how
604 BV effectiveness might be enhanced in the field through biotic interactions. Although the
605 research has not yet been exploited in terms of improving our use of BV on most crops, the
606 ecology of host pathogen interactions is envisioned to be a way forward to developing new
607 strategies for novel BV deployment (Waage, 1997).

608

609 ***2.3 Societal factors and their role in determining the adoption of insect viruses***

610 Environmental pressures and consumer health concerns have been increasingly focused on the
611 health and environmental impacts of crop protection products and the well-established safety of
612 BV (OECD, 2002; Leuschner et al., 2010; Mudgal et al., 2013) is a major advantage. While
613 public surveys have not shown that food safety risks are perceived as a major concern, they are a
614 significant issue for up to 25% of consumers (Food Standards Agency 2013). The recent
615 controversy over neonicotinoids in the EU has shown that public concerns can drive significant
616 changes in crop protection policy even if the scientific evidence is controversial (Gross 2013).
617 These concerns in the EU have led to the sustainable use directive (SUD), a policy of reducing
618 reliance on chemical pesticides and mandatory adoption of integrated pest management (IPM)
619 for all crops (Hillocks 2012) . In addition, chemical pesticides must be reregistered, which has
620 led to a reduction in the number of chemical crop protection products allowed from

621 approximately 1,000 in 1993 to less than 330 today (European Commission 2009). These
622 measures are undoubtedly increasing the potential for use of BV; however, increased demand for
623 new BCA elicit serious concerns that the supply of new products remains inadequate to replace
624 the chemical pesticides being withdrawn (Hillocks 2012).

625 One barrier to increasing the supply of commercial BV products is registration (Chandler et
626 al 2011; Ehlers 2011; Lapointe et al., 2012). Regulatory authorities in many countries and
627 jurisdictions are unable to complete registration of BV products in a timely, economic and
628 transparent manner (Kabaluk, 2010; Gwynn, 2014). This may be due to bureaucratic inertia in
629 some cases, but often the absence of the appropriate biological expertise among regulators has
630 been cited as a significant constraint (Chandler et al., 2011). Some regulatory bodies such as the
631 US EPA as appear to be proactive in developing the appropriate expertise and a positive ethos to
632 facilitate the registration of new BV products through effective fast track systems (Bailey et al.,
633 2010) but the EU, although sponsoring active reviews of microbial pesticide registration (Ehlers
634 2011), has not yet implemented a specific fast track for microbial pesticides. EU registration has
635 long timelines and higher costs that deter registrations, especially by the small-medium size
636 enterprises (SMEs) that are frequently in the forefront of microbial pesticide innovation and
637 develop 80% of novel microbial pesticide products (Chandler et al., 2011; Ravensberg, 2012).
638 The use of microbial pesticides has not yet generated serious public concern, although the issue
639 has been mentioned by some authors such as Lapointe et al. (2012), attitudes may change as BV
640 use expands.

641

642 ***2.4 Insect viruses in the next decade***

643 There is a clear need for need for new BV products active against pests that may increase in
644 impact as chemical actives are withdrawn. Most BV products recently commercialised or being
645 brought to market are based on species that are well known and have been studied for at least 30
646 years. There is a serious concern about the dearth of novel BV species. Given the limited
647 progress since 2001 in identifying new BV, it is far from clear that new crop protection products
648 will emerge without increased funding for research and development of BV against new and
649 emerging threats arising from chemical withdrawal. There is also a need for new technology to
650 mass-produce BV at costs that appropriate for large-scale use of BV in field crops. Although *in*
651 *vivo* production is an established technology, it is far from certain that it can be expanded to meet
652 the quantum leap in production that is needed to replace chemical pesticides for major field
653 crops. It remains to be seen if *in vitro* systems will overcome the scaling up cost and quality
654 issues that have prevented these from be adopted by commercial producers. The other key need
655 is to develop a better understanding of how BV interact with other BCA to identify synergys that
656 can enhance their overall performance. Many believe that the BV, like other BCA, will never
657 achieve their full potential until they are deployed as components of ecologically based IPM
658 systems rather than substitutes for chemical insecticides.

659

660 **3. Entomopathogenic Bacteria**

661 **3.1 *Bacillus thuringiensis* (Bt)**

662 *3.1.1 Background and overall status.* An enormous number of bacterial species have been
663 reported from pest and beneficial insects (Jurat-Fuentes and Jackson, 2012) but a relatively small
664 number of entomopathogenic bacteria have been commercially developed for control of insect

665 pests of crops, forests, turf, humans, and livestock. These include several *Bacillus thuringiensis*
666 (Bt) sub-species, *Lysinibacillus (Bacillus) sphaericus*, *Paenibacillus* spp. and *Serratia*
667 *entomophila* (Table 2). The most widely used bacteria for control of numerous insect pests are Bt
668 subsp. (Glare and O'Calaghan, 2000; Federici, 2005; Bravo et al., 2011; Glare et al., 2012;
669 Jurat-Fuentes and Jackson, 2012).

670 Highlights of the history and commercial development of Bt are presented by Beegle and
671 Yamamoto (1992), Federici (2005) and Davidson (2012). Sub-species represent about 98% of
672 formulated sprayable bacterial microbial pesticides, due in part to the wide host range with
673 activity against Lepidoptera, Diptera (Nematocera), Coleoptera (Chrysomelidae and
674 Scarabaeidae), additional species in other orders of insects and other pest invertebrates (mites
675 and nematodes) (Carneiro et al., 1998; Schnepf et al., 1998; Wei et al., 2003; van
676 Frankenhuyzen, 2009). Three notable examples are Bt strains with activity for scarab larvae (Bt
677 subsp. *japonensis* (Buibui strain), Suzuki et al., 1992); two sawfly species *Diprion pini* and
678 *Pristiphora abietina* (Porcar et al., 2008); and root knot nematodes, *Meloidogyne* spp. (Chen et
679 al., 2000; Li et al., 2008; and Khan et al. 2010).

680 Additional prospection and development will most likely provide *B. thuringiensis* isolates
681 with an even broader spectrum of activity. Crickmore et al. (2014) provide a continually updated
682 list of Bt toxins with links to information on additional host insects and other organisms that are
683 susceptible to them. There are currently no less than 73 families of crystal (CRY) toxins
684 comprising a total of 732 toxins, 3 families of cytotoxic (Cyt) proteins including 38 different
685 toxins and 125 Vegetative Insecticidal Proteins (VIPs) belonging to 4 different families
686 (Crickmore et al., 2014).

687 The primary reason for the utilization of Bt is that it combines advantages of chemical
688 pesticides and microbial pesticides. Like chemical pesticides, Bt is fast acting, easy to produce at
689 low cost, easy to formulate, and has a long shelf life. It also can be applied using conventional
690 application equipment and systemics (i.e. in transgenic plants). Unlike broad spectrum chemical
691 pesticides, *B. thuringiensis* toxins are selective and negative environmental impact is very
692 limited (Glare and O'Callaghan, 2000; Lacey and Siegel, 2000; Hokkanen and Hajek, 2003;
693 Lacey and Merritt, 2003; Birch et al., 2011).

694

695 3.1.2 Control of pest insects with *B. thuringiensis* microbial pesticide products

696 3.1.2.1 Crops and orchards: Bt has no pre-harvest spray interval and can be applied until harvest
697 begins. It has minimal or no impact on beneficial organisms in these agroecosystems; however,
698 although efficacious, it is sensitive to solar degradation and requires frequent application.

699 *B. thuringiensis* subsp. *kurstaki* (Btk, Dipel) and to a lesser extent *B. thuringiensis* subsp.
700 *aizawai* (Xentari) are used for control of lepidopteran pests in orchards and in vegetable
701 production (Glare and O'Callaghan, 2000; Lacey and Shapiro-Ilan, 2008; Glare et al., 2012). It is
702 used extensively in organic vegetable production and is increasingly being utilized by
703 conventional growers. Control of a plethora of pest Lepidoptera is common in row crops
704 including crucifers, solanaceous vegetables, cucurbits, corn, legumes, soybeans, cotton, and
705 others. The implementation of Btk for control of orchard pests, particularly leafrollers and other
706 defoliators, was described by Lacey et al. (2007) and Lacey and Shapiro-Ilan (2008).

707 A multitude of papers on applied research and use of Bt-based products for protection against
708 lepidopteran pests of vegetables and tree fruit have been published since 2000 and many are
709 referenced by Glare and O'Callaghan (2000), Metz (2003), Lacey and Kaya (2007), Jurat-

710 Fuentes and Jackson (2012). Kabaluk and Gazdik (2005) provide a directory of biopesticides that
711 includes producers of several commercial Bt products for control of Lepidoptera.

712 Control of coleopteran pests in crops using commercially produced *B. thuringiensis* is limited
713 to beetles in the family Chrysomelidae, principally the Colorado potato beetle, *Leptinotarsa*
714 *decemlineata* (Wraight et al., 2007b, 2009). The beetle-active toxin (Cry 3Aa) is produced by *B.*
715 *thuringiensis* subsp. *tenebrionis* (Btt). It can provide an effective means of control, especially
716 when applied at regular intervals against early instars. Btt was rapidly developed as a microbial
717 pesticide in the late 1980s and early 1990s (Gelernter and Trumble, 1999; Gelernter, 2002).
718 However, several factors, most notably competition with neonicotinyl insecticides, resulted in its
719 near disappearance from the marketplace (Gelernter, 2002). The Cry3Aa toxin expressed in
720 transgenic potato provides complete protection from *L. decemlineata* but current public
721 opposition to transgenes in food has resulted in removal of transgenic potato from the market in
722 North America and Europe. Transgenic ‘Spunta’ potato lines with the *cryIIa1* gene were
723 completely resistant to potato tuberworm in laboratory and field tests (Douches et al., 2002,
724 2011).

725
726 *3.1.2.2 Stored product pests:* Several pest insects attack stored grain, fruit, nuts, potatoes and
727 other stored food products. Btk products have been used to control several of these pests (Lord et
728 al., 2007; Shapiro-Ilan et al., 2007; Kroschel and Lacey, 2008). Good efficacy of Btk has been
729 demonstrated and protocols have been published for the evaluation of Btk control against *Plodia*
730 *interpunctella* and other lepidopteran pests of stored grain (Lord et al., 2007). Despite the
731 massive volume of grain in grain silos, only the top 10 cm of grain require treatment (Lord et al.,
732 2007). Kroschel and Lacey (2008) and Lacey and Kroschel (2009) described examples of large-

733 scale implementation of Btk in several countries for control of the potato tuber moth,
734 *P. operculella* in rustic stores of potato tubers.

735
736 *3.1.2.3 Forests:* Btk is the principal non-chemical means of control for lepidopteran pests of
737 forests and development in the 1970s and 1980s facilitated broader commercial development in
738 the 1980s and 1990s (van Frankenhuyzen et al., 2007). Btk has been used extensively against the
739 spruce budworm, (*Choristoneura fumiferana*) and gypsy moth (*Lymantria dispar*) (van
740 Frankenhuyzen et al., 2000; Bauce et al., 2004; van Frankenhuyzen et al., 2007). Protocols for
741 the evaluation of Btk and other isolates of Bt for control of *C. fumiferana* and *L. dispar* are
742 presented by van Frankenhuyzen et al. (2007). Btk has also been used for control of other
743 lepidopteran forest defoliators across North America and Europe including *Thaumetopoea*
744 *processionea*, *T. pityocampa*, *Lymantria monacha*, *Dendrolimus sp.* *Bupalus piniaria*, *Panolis*
745 *flammea*, *Tortrix viridana*, *Operophtera brumata*, *Dioryctria abietella*, *Lambdina fiscellaria*
746 *fiscellaria*, *Choristoneura occidentalis*, *C. pinus pinus*, *Orgyia leucostigmata*, *O. pseudotsugata*,
747 and others (Fuxa et al., 1998; van Frankenhuyzen, 2000).

748 The only non-lepidopteran forest pest insects that are susceptible to Bt are in the coleopteran
749 family Chrysomelidae. Bauer (1992) bioassayed Btt for larvicidal activity against the imported
750 willow leaf beetle, *Plagioderma versicolora*, reared on poplar (*Populus*) or willow (*Salix*). Good
751 larvicidal activity of the bacterium was only observed on the larvae reared on poplar. Genissel et
752 al. (2003) reported on the deleterious effects of feeding *Chrysomela tremulae* larvae and adults
753 on leaves from transgenic poplar expressing the *cry3Aa* gene from Btt. No large scale field trials
754 have yet been conducted with Btt for control of chrysomelids in forests.

755

756 3.1.2.4 *Lawn and turf*: Klein et al. (2007) and Koppenhöfer et al., (2012) provide overviews of
757 the use of Bt subsp. for control of turf pests. Btk and Bt subsp. *aizawai* are registered for
758 control of sod webworms and armyworm, *Mythimna (Pseudaletia) unipuncta*, in turf. Although
759 not widely used for control of these pests, Bt strains provide some control if used when early
760 instars are present and applications are made during the early evening to avoid as much UV
761 degradation as possible. Oestergaard et al. (2006) demonstrated control of the European crane
762 fly, *Tipula paladosa*, with *B. thuringiensis* subsp. *israelensis* (Bti) applied against early instars;
763 however, there are no reports in the literature of routine use of Bti for crane fly control in turf.
764 The Bt subsp. *japonensis* (Buibui strain) is insecticidal for the Japanese beetle, *Popillia japonica*,
765 and other scarab species that are turf pests (Suzuki et al., 1992; Alm et al., 1997; Koppenhöfer et
766 al., 1999, 2012; Bixby et al., 2007). Koppenhöfer et al. (1999) observed an additive and
767 synergistic interaction between entomopathogenic nematodes (*Sterinernema* spp. and
768 *Heterorhabditis bacteriophora*) and Bt subsp. *japonensis* (Buibui strain) for control of the grub
769 *Cyclocephala* spp. An advantage of Bt subsp. *japonensis* over *Paenibacillus popilliae*, another
770 bacterium used for *P. japonica* control, is that it can be grown on artificial media and has a
771 broader host range within the Scarabaeidae.

772

773 3.1.2.5 *Medically important insects*: Several species of culicid mosquitoes (Culicidae) are
774 widespread pests, many of which transmit disease causing agents such as *Plasmodium* spp.
775 (malaria), filaroid nematodes (elephantiasis, Mansonellosis) and viruses (yellow fever, dengue,
776 and several that cause encephalitis) (Foster and Walker, 2009). The aquatic habitats in which Bti
777 is used for mosquito control are extremely diverse in terms of location (salt marsh, tree holes,
778 wetlands, containers, and a variety of other habitats) and water quality (Skovmand et al., 2007).

779 Black flies (Simuliidae) are always found in lotic habitats (rivers, streams, creeks) (Adler et al.,
780 2004; Adler and McCreadie, 2009) and, in addition to their highly pestiferous activity, some
781 species transmit the filaroid nematodes that cause human and bovine onchocerciasis (Adler and
782 McCreadie, 2009). Bti is the only Bt subsp. that is commercially produced for control of vector
783 and pestiferous Diptera in both the Culicidae (Lacey, 2007; Despres et al., 2011) and Simuliidae
784 (Adler et al., 2004; Skovmand et al., 2007). Although Bti is very efficacious, its persistence in
785 the environment, especially those with high organic content, is short lived and requires frequent
786 reapplication. Dense foliar canopy and rapid settling of toxin in deeper lentic habitats decrease
787 the amount of inoculum reaching the habitat and decreased time for larval exposure. Toxin is
788 carried shorter distances in shallow streams with large substrate to water volume ratios (wide and
789 shallow). Large rivers can result in effective carry of the toxin up to 30 kilometers. Further
790 improvements in formulations and delivery systems are expected to increase efficacy in
791 mosquito and black fly habitats.

792

793 *3.1.3. Production of B. thuringiensis.* The nutrient media and conditions under which Bt and *L.*
794 *sphaericus* are produced can markedly influence larvicidal activity. Guidelines and typical media
795 ingredients for shake flask, stir tank and deep tank fermentation are presented by Beegle et al.
796 (1991), Lisansky et al. (1993), and Couch (2000). Although there is continued improvement in
797 fermentation technology for *B. thuringiensis*, information on any specific changes in methods
798 and media by industry nearly always is proprietary (Couch, 2000). However, there have been
799 developments in small scale production using unique media components such as local raw
800 ingredients of plant and animal origin and bi-products (such as whey) which provide inexpensive

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801 nitrogen and carbon sources for the production of Bt and *L. sphaericus* (Aranda et al., 2000;
802 Lacey, 2007).

803
804 *3.1.4. Transgenic crops or Bt-crops.* The largest market progress over the last two decades was
805 associated with the development of a Bt product different from the microbial pesticides, the Bt
806 transgenic crops. The Cry toxins and VIPs are the only toxins currently used in commercial
807 insecticidal transgenic crops. VIP toxins are only found in transgenics but several Cry toxins
808 produced by Bt-crops are the same as those produced for Bt microbial pesticides such as Dipel or
809 Xentari. GM crops have been the most rapidly adopted production technology in agriculture
810 (Brookes and Barfoot, 2013; James, 2013). Although implementation has not been without
811 controversy, wide acceptance is due to specificity to insects and high efficacy of *B. thuringiensis*
812 Cry toxins, and safety for consumers and non-target organisms (Shelton et al., 2002; Bravo et al.,
813 2011). A large diversity of toxin genes that are relatively simple to clone and express are found
814 in different *B. thuringiensis* strains. The toxin genes are distributed into families that are easy to
815 characterize and the toxins are organized into clearly distinguishable functional domains (Bravo
816 et al., 2007). These traits not only make the mode of action (MOA) of the toxins easier to
817 elucidate but also make both toxins and toxin genes good models for genetic engineering. Early
818 in the 1980's, *B. thuringiensis* was already a commercially successful product. *B. thuringiensis*
819 insecticidal proteins were some of the only gene products meeting the technical and ethical
820 requirements for plant biotechnology. Subsequently, *B. thuringiensis* toxins became the most
821 promising source for development insect-resistant transgenic plants (Kennedy, 2008).

822 Global Bt-crop acreage has increased enormously in the last two decades, reaching 175
823 million ha in 2013 (Choudery and Guar, 2010; Brookes and Barfoot, 2013; James, 2013). The

824 adoption rate was 100% or near 100% in 2013 for all major transgenic crops in the primary
825 producing countries. Stabilization of adoption rate and area planted are therefore expected in the
826 coming years (James, 2013).

827 The increased use of Bt-cotton and Bt-corn has resulted in a significant decrease in the use of
828 chemical insecticides (Phipps and Park, 2002; Brookes and Barfoot, 2013), particularly in cotton
829 (Huanga et al., 2003; Edwards and Poppy, 2009; Krishna and Qaim, 2012). However, transgenic
830 technologies also compete with sprayable formulations of Bt due to the similarity of toxins used
831 and result in a lower commercial share left to Bt microbial pesticides. Furthermore, while
832 reducing the overall market for chemical insecticides, widespread adoption of Bt crops can
833 increase the market for herbicides as new generations of transgenic plants expressing stacked Bt
834 and herbicide-resistance genes are now on the market (James, 2013). Given the widespread
835 environmental concerns over broad-spectrum chemical pesticides, it is possible that GM crops
836 deploying pest specific safe gene products such as Bt toxins may finally be considered a more
837 environmentally acceptable solution for pest control than the development and widespread
838 application of newer chemical pesticides.

839 Given the high cost of developing and deploying a new transgenic crop, currently estimated
840 as \$136 million (McDougall, 2013; Mumm, 2013), it will not be economically viable to develop
841 GM varieties for all crops, including many minor use or locally important crops, or to control all
842 specific pests and diseases (Shelton, 2012). Non-GM crop diversity and local varieties must be
843 maintained for many reasons ranging from differing climates and specific cultural food practices
844 to the need for a diverse genetic base for disease tolerance. Because not all crops and varieties
845 will be transgenic, other conventional but still environmentally friendly means of control must be
846 retained and developed. Among these should be new Bt-based microbial pesticides, as well as

847 other entomopathogen-based pesticides. However, niches for microbial pesticides must address
848 new issues to avoid competition with, for example, focusing on a mosaic of secondary pest
849 problems. Microbial pesticides for forestry and vector control may be an exception to treatment
850 of row crops because competition with transgenics does not exist. We predict that microbial
851 pesticides, such as sprayable and other Bt formulations, will continue to have a successful future
852 in the coming decades.

853

854 *3.1.5. Controversy around Bacillus thuringiensis toxins in GM crops.* In this section we address
855 the biological aspects of the controversy over the use of Bt crops and focus on safety and
856 environmental concerns. Divisive socio-economic and political issues will not be covered and
857 should be the subject of a separate forum discussion. The Bt toxins are essential in the
858 deployment of a number of major insect resistant GM crops and, therefore, *B. thuringiensis*
859 microbial pesticides were also involved in the extensive controversy around the safety and
860 efficacy of GM crops. A notable example has been concern about effects of Bt toxins on the
861 monarch butterfly, *Danaus plexippus*. Pollen from Bt-maize dusted onto milkweed under
862 laboratory conditions was reported to produce mortality in *D. plexippus* larvae (Losey et al.,
863 1999). Follow up research determined that the deleterious results were related to a specific maize
864 variety (Bt176, no longer in commercial use) and that there was no negative impact to monarchs
865 under field conditions (Hellmich et al., 2001; Minorsky, 2001; Pleasants et al., 2001; Sears et al.,
866 2001; Stanley-Horn et al., 2001; Tschenn et al., 2001; Zangerl et al., 2001; Dively et al., 2004;
867 Anderson et al., 2005). Nevertheless, the controversy generated a widespread perception that Bt-
868 engineered crops are dangerous for the environment. This issue was revived 10 years later when
869 France and Germany banned the Bt-maize variety MON810 on the basis of a threat to *D.*

870 *plexippus*, despite the facts that MON810 was found to be harmless to monarch larvae and *D.*

871 *plexippus* is not found in Europe (Ricroch et al., 2010).

872 A second example relating to the health impact of Bt crops is the “StarLink case” (Bucchini
873 and Goldman, 2002; Bernstein et al. 2003). In this instance, the StarLink product, a feed-
874 registered insect-resistant Bt-maize engineered with the Cry9Ca toxin, was found in human food.
875 This was followed by reports of allergic shock in consumers, although follow-up studies by the
876 Centers for Disease Control failed to confirm any link to the Cry9Ca toxin (CDC, 2001).
877 Nevertheless, problems were confirmed in the management and control of feed-registered BT-
878 corn products that allowed them to be comingled with food for human consumption (Bucchini
879 and Goldmann, 2002). The controversy subsequently led to a serious loss of market share for
880 U.S. corn growers (Schmitz et al., 2005). An additional consequence of the controversy has
881 resulted in stories implicating Bt crops either in health scares or as contributors to disastrous crop
882 failures (Tirado, 2010; Coalition for GM free India, 2012). Several of these stories subsequently
883 were shown to be untrue (Gruere et al., 2008; Brookes and Barfoot, 2013).

884 Bt microbial pesticides, while accepted in pest control, organic agriculture and vector
885 control, also have become subjects of debate in the crop biotechnology arena and have been
886 represented by some as a threat to human or environmental health. For example, Poulin et al.
887 (2010) and Poulin (2012) demonstrated the negative trophic effect of Bti treatment for mosquito
888 control on non-target fauna. The reduction of mosquitoes and chironomids and consequently
889 their predators as prey of breeding house martins, *Delichon urbicum*, resulted in reduced clutch
890 size and fledgling survival. Among other measures, Poulin et al. (2010) recommended
891 suspension of mosquito control in certain habitats. We believe that such measures should take

892 into account the effect of mosquito reduction on quality of life for humans and domestic animals,
893 but most importantly the interruption of disease transmission.

894 A positive aspect of the debates on the safety of Bt products is that they have prompted
895 renewed studies on actual health and environmental effects of Bt toxins. These have shown that
896 commercially approved Bt products and Bt genes are safe and can have positive benefits for the
897 environment, mostly through the reduced use of chemical pesticides and lack of effects on non-
898 target organisms, (Saxena, and Stotsky, 2001; Phipps and Park, 2002; Shelton et al., 2002, 2007;
899 Lacey and Merritt, 2003; O'Callaghan et al., 2005; Wu et al., 2005; Romeis et al., 2006; Marvier
900 et al., 2007; Roh et al., 2007; Chen et al., 2008; Kumar et al., 2008; Wolfenbarger, et al. 2008).

901
902 *3.1.6. Insect resistance and mode of action of Bt toxins.* One of the most important aspects to
903 address with Bt-based products and Bt crops is resistance management. *B. thuringiensis* shares
904 with chemical pesticides the negative trait of producing resistance to the toxic effects in target
905 insect populations. Resistance is the interruption of the mode of action (MOA) of any pesticide,
906 and understanding insect resistance and proposed insect resistance strategies requires first
907 summarizing the MOA. This section is intended to underline the sequential nature of the MOA
908 of *B. thuringiensis* insecticidal proteins and its susceptibility to resistance. Resistance can result
909 from the interruption of any of the step described in this section and, indeed, several mechanisms
910 of resistance have been described. The MOA is well understood for a limited number of Bt
911 toxins, including the Cry and Cyt families used in microbial pesticides, and the Cry and VIP in
912 transgenic crops.

913 The MOA of Cry proteins is by far the best known (Whalon and Wingerd, 2003; Bravo et al.,
914 2007, 2011; Pigott and Ellar, 2007, Vachon et al., 2012). Pathogenesis begins with the ingestion

915 of the Bt crystal. The crystal, which contains protoxins, is then solubilized by the alkaline pH of
916 the insect midgut and the soluble protoxins are activated by midgut serine proteases releasing the
917 active toxin. The structure of these activated toxins has been determined for several families. In
918 the Cry1 family, three functional domains have been identified (Li et al., 1991; Grochulski et al.,
919 1995; Galitsky et al., 2001; Morse et al., 2001; Boomserm et al., 2005, 2006) (Figure 2). Domain
920 I consists of 7 alpha helices organized in a barrel-like structure and is involved in pore formation.
921 Domains II and III are comprised of layers of beta sheets that recognize specific binding sites at
922 the surface of the midgut brush border (Pigott and Ellar, 2007). These binding sites have been
923 identified mostly as aminopeptidase N-like proteins (APN) and cadherin-like proteins, although
924 other putative receptors such as alkaline phosphatases (ALP), glycolipids or a 270-kda
925 glycoconjugate (Pigott and Ellar, 2007) have been identified. Following specific binding, the
926 toxin undergoes a change of conformation and inserts into the midgut membrane to form an ionic
927 channel or pore (Knowles and Ellar, 1987; Vié et al., 2001; Bravo et al., 2004; Vachon et al.,
928 2012) transporting ions with their free charged-amino acids (Masson et al., 1999; Vachon et al.,
929 2002, 2004; Girard et al., 2009; Lebel et al., 2009). Ion transport triggers a physiological
930 imbalance leading to the death of the cell, destruction of the midgut and ultimately death of the
931 insect. This process of ionic imbalance, originally described as colloid-osmotic lysis (Knowles
932 and Ellar, 1987; Bravo et al., 2004), is probably not the only mechanism involved in cell death.
933 Signaling pathways that follow receptor binding recently have been described (Zhang et al.,
934 2006). These pathways are triggered upon receptor activation by protein binding and initiate cell
935 death mechanisms. However, these two mechanisms are not exclusive and could both contribute
936 to the overall toxicity of Cry toxins as suggested by Jurat-Fuentes and Adang (2006) and
937 discussed by Vachon et al. (2012).

938 Resistance to Bt toxins was first reported in *Plodia interpunctella*, an insect pest of stored
939 grain, by McGaughey (1985; 1994). Field resistance has since been reported in diamond back
940 moth, *Plutella xylostella*, and cabbage looper, *Trichoplusia ni*, and several major insect pests
941 under laboratory selection (Tabashnik, 1994; Moar et al., 1995; Rahman et al., 2004, Shelton et
942 al., 2007; Furlong et al., 2013). In common with Bt microbial pesticides, Bt crops also are
943 susceptible to resistance problems and a number of cases have been reported, particularly with
944 first generation single gene constructs (Rhaman et al., 2004, Shelton et al., 2007; Tabashnik,
945 2008; Tabashnik et al., 2008a, 2008b, 2009, 2013). Modification of the Bt binding sites is the
946 most commonly reported resistance mechanism, however other mechanisms affecting different
947 steps of the MOA have been described and can potentially develop (Frutos et al., 1999; Griffitts
948 and Aroian, 2005; Heckel et al., 2007). A key point is that resistance affects both microbial
949 pesticides and transgenic crops in the same way, and cross-resistance to other similar toxins used
950 in both modes of delivery could occur.

951
952 *3.1.7. Future directions.* Since *B. thuringiensis* remains the primary sprayable microbial
953 pesticide, the increasing demand for organic products should encourage the development of
954 additional Bt products. Demand would also be driven partly by safety legislation requiring
955 reduction of the number of chemical pesticides. The future sustainability of Bt crops will rely on
956 a combination of multistacked toxin genes and refugia to delay resistance (Caprio and
957 Summerford, 2007; Tabashnik, 2008, Head and Greenplate, 2012; Storer et al., 2012).

958 Addressing resistance and resistance management will depend on detailed knowledge of the
959 MOA of Bt toxins (Griffitts and Aroian, 2005; Shelton et al., 2007). Multiple-gene constructs
960 targeting different binding sites is the basis for the gene pyramiding that underlies the

961 development of novel generations of Bt crops (Shelton et al., 2002). In addition to discovery of
962 more efficacious isolates and toxins, an increase in the use of Bt products and transgenes will
963 rely on innovations in formulation, better delivery systems and ultimately, wider public
964 acceptance of transgenic plants expressing Bt toxins.

965

966 **3.2 *Lysinibacillus (Bacillus) sphaericus***

967 Although less commonly used than Bti for control of mosquitoes, *L. sphaericus* offers some
968 advantages that Bti does not. Only the IIA sub-group includes isolates with larvicidal activity for
969 mosquitoes (Charles et al., 1996). The moiety responsible for mosquito larvicidal activity in
970 serovar 5a5b isolates of *L. sphaericus* is a binary toxin (Charles et al., 1996) with both proteins
971 required for full toxicity. The individual roles of the toxin components were elucidated by
972 Charles et al. (1997) and Schwartz et al. (2001). As with Bti, ingested toxins are solubilized in
973 the alkaline midgut and cleaved to the active moiety by proteases. The two component proteins
974 of the toxin, BinA (42 kDa) and BinB (51 kDa) bind to specific receptors on the brush border of
975 epithelial cells of the gastric caecum and midgut and cause pore formation resulting in disruption
976 of osmotic balance, lysis of the cells, and ultimately death of the insect (Charles et al., 1996). *L.*
977 *sphaericus* binary toxin is more specific and narrower in range than the Bti toxins; it is
978 principally active against *Culex* mosquitoes. Several *Aedes* species in the *Stegomyia* group (such
979 as *Aedes aegypti*) are not susceptible to *L. sphaericus* formulations.

980 Protocols for the short-term evaluation of *L. sphaericus* formulations in the field are similar
981 to that of Bti (Skovmand et al. 2007). Biotic and abiotic factors that influence the larvicidal
982 activity of Bti and *L. sphaericus* include the species of mosquito and their respective feeding
983 strategies, rate of ingestion, age and density of larvae, habitat factors (temperature, solar

984 radiation, depth of water, turbidity, tannin and organic content, presence of vegetation, etc.),
985 formulation factors (type of formulation, toxin content, how effectively the material reaches the
986 target, and settling rate), storage conditions, production factors, and means of application and
987 frequency of treatments (Lacey, 2007). *L. sphaericus* formulations have been utilized
988 predominantly in organically enriched habitats, but they are also active against numerous
989 species, and across several genera in habitats with low organic enrichment. The bacterium has
990 been shown to persist longer than Bti in polluted habitats and can recycle in larval cadavers
991 (Lacey, 2007). A disadvantage of *L. sphaericus* is the development of resistance in certain
992 populations of *Culex quinquefasciatus* and *Cx. pipiens*. Low to extremely high levels of
993 resistance to the *L. sphaericus* binary toxin have been reported in populations of *Cx.*
994 *quinquefasciatus* in India, Brazil, China, Thailand, Tunisia and France (Charles et al., 1996;
995 Lacey, 2007). The combination of *L. sphaericus* and toxin genes from Bti increases the host
996 range of the bacterium and could offer a means of combatting resistance (Federici et al., 2007).

998 **3.3 *Paenibacillus* species**

999 *Paenibacillus* spp. are spore-forming obligate pathogens of larval coleopterans in the family
1000 Scarabaeidae (Klein, 1992; Klein et al., 2007; Koppenhöfer et al. 2012). The disease caused by
1001 these bacteria is known as milky disease due to the milky appearance of the hemolymph in
1002 infected larvae. Spores of the bacterium must be ingested in order to invade the hemocoel and
1003 produce an infection. Natural epizootics have been observed in *P. japonica*, but variable results
1004 have been obtained after application of spore powders. In some cases, epizootics have been
1005 induced following applications (Klein, 1992), in others, little or no activity was observed (Klein
1006 1992, Lacey et al., 1994). The spores have been known to persist for several years in the soil

1007 (Klein, 1992). *P. popilliae* was the first microbial pesticide registered in North America (1948)
1008 for control of *P. japonica* (Klein, 1992), but large-scale commercial development has been
1009 limited due to the requirement for *in vivo* production and the narrow host range within the
1010 Scarabaeidae. A breakthrough in *in vitro* production of *P. popilliae* and development of strains
1011 effective against other important scarab species (e.g., *Cyclocephala* spp., *R. majalis*, *A.*
1012 *orientalis*, and *Melolontha melolontha*) would significantly improve the marketability of these
1013 bacteria.

1014

1015 **3.4 *Serratia entomophila***

1016 The endemic non-sporeforming bacterium *Serratia entomophila* (Enterobacteriaceae) was
1017 discovered and developed in New Zealand, and is used for control of the New Zealand grass
1018 grub, *Costelytra zealandia* (Jackson et al. 1992; Jackson, 2007). Cultivation of pastures for
1019 cropping and re-sowing generally kills grass grubs and eliminates pathogenic strains of bacteria,
1020 leaving new pastures vulnerable to pest attack. This provides an opportunity for augmentative
1021 biological control, where *S. entomophila* is applied to *C. zealandia* populations to promote
1022 epizootics and prevent the occurrence of pasture damage.

1023 Strains of the *Serratia* spp. cause amber disease in *C. zealandia* (Jackson et al., 2001). The
1024 bacterium must be ingested for toxin production to be initiated and disease progression is
1025 accompanied by a cessation of feeding, clearance of the gut and a halt in the synthesis of
1026 digestive enzymes. Infected larvae take on a distinctive amber coloration prior to death (Jackson
1027 et al., 2001). *Serratia entomophila* is now commercialized as a stabilized dry granular product
1028 Bioshield™ (Jackson et al., 1992, 2001). The formulation is stable under ambient conditions for
1029 several months and is applied using a conventional seed drill, which has enhanced adoption of

1030 this microbial pesticide by the pastoral sector in New Zealand (Jackson, 2007). Recycling of the
1031 disease through grass grub larvae produces an endemic population of pathogenic bacteria
1032 preventing recurrent damaging outbreaks of the pest. The technology for stabilization of this
1033 non-spore forming bacterium could be useful in the future for other non-spore forming
1034 entomopathogenic species of bacteria.

1035

1036 **3.5 *Chromobacterium subtsugae***

1037 Martin et al., (2007a, 2007b) isolated *Chromobacterium subtsugae*, a new species and genus of a
1038 motile, Gram-negative bacterium, with *per os* toxicity to larval Colorado potato beetle,
1039 *Leptinotarsa decemlineata*, adults of the corn rootworms, *Diabrotica* spp., and the southern
1040 green stinkbug, *Nezara viridula*. Encouragingly, live bacteria were not needed for toxicity to *N.*
1041 *viridula* adults (Martin et al., 2007b). Marrone Bio Innovations (MBI) has registered a biological
1042 insecticide/miticide (Grandevo[®]) containing *C. subtsugae* strain PRAA4-1T and spent
1043 fermentation medium for use on edible crops, ornamental plants and turf against defoliating
1044 caterpillars and certain Coleoptera (EPA Reg. No.: 84059-17-87865). MBI also reported the
1045 formulation to have multiple effects such as reduced fecundity and oviposition, reduced feeding
1046 and activity as a stomach poison on aphids, psyllids, whiteflies, *Lygus*, mealybugs, thrips and
1047 phytophagous mites. Genes encoding toxins and VIPs of this bacterium could conceivably be
1048 candidates for incorporation into GM crops for targeting a broad pest host range.

1049

1050 **4. Entomopathogenic Fungi**

1051 **4.1 Background and overall status**

1052 Fungi are the predominant natural pathogens in arthropod populations. Observations of
1053 epizootics among insect populations are common, indicating the great potential of these
1054 microbes for regulation of pestiferous species. Entomopathogenic fungi infect their hosts through
1055 the external cuticle and are pathogenic to both soft- and hard-bodied insects, as well as a range of
1056 other arthropods including Acari (ticks, mites). Cuticular invasion also enables fungi to infect
1057 sucking insects such as aphids, whiteflies, psyllids and scales (Burges, 2007; McCoy et al., 2009;
1058 Lacey et al., 2011). Consequently, fungi have been widely evaluated as control agents for a
1059 diverse variety of noxious arthropods of agricultural (including forestry and livestock) and
1060 horticultural importance (Chandler et al., 2000; Shah and Pell, 2003; Brownbridge 2006; Abolins
1061 et al. 2007; Charnley and Collins 2007; Jaronski 2007; Maniania et al., 2007; Wraight et al.,
1062 2007a; Zimmermann 2007a, b; 2008; Alves et al., 2008; Kaufman et al. 2008; James 2009; Glare
1063 et al., 2010; Goettel et al., 2010). Recent discoveries of the effects of entomopathogenic fungi on
1064 adult mosquitoes, including the prevention of development of vectored human pathogens within
1065 fungal infected mosquitoes, has resulted in an upsurge of research on their potential for control
1066 of mosquito-borne diseases such a malaria (Blanford et al., 2005, 2009; Scholte et al., 2003,
1067 2004. 2005; Kikankie et al., 2010). Although entomopathogenic fungi traditionally have been
1068 regarded exclusively as pathogens of arthropods, recent studies suggest that they play additional
1069 roles in nature. Many are now known to be plant endophytes, plant disease antagonists,
1070 rhizosphere colonizers, and plant growth promoters (Vega et al., 2009; Behie et al., 2012; Jaber
1071 et al., 2014).

1072 Several hypocrealean entomopathogenic fungi are important constituents of natural- and
1073 agro-ecosystems and appear to be ubiquitous inhabitants of soils worldwide. They have been
1074 recovered from a diverse array of geographic, climatic, and agro-ecological zones (Bidochka et

1075 al., 2001, 2002; Shimazu et al., 2002; Keller et al., 2003; Shapiro-Ilan et al., 2003a; Meyling and
1076 Eilenberg 2006a, b; 2007; Jaronski 2007; Quesada-Moraga et al 2007; Zimmermann 2007a, b;
1077 2008; Inglis et al., 2008, 2012; Reay et al., 2008, Meyling et al., 2009; Scheepmaker and Butt,
1078 2010). Fungi such as *Beauveria bassiana* s.l. and *Metarhizium anisopliae* s.l. are commonly
1079 found in both cultivated and undisturbed soils, although their natural distribution appears to be
1080 linked to habitat (Bidochka et al., 2001; Keller et al., 2003; Meyling and Eilenberg, 2006a;
1081 Meyling et al., 2009), and soil populations are influenced by agricultural practices (Hummel et
1082 al., 2002; Jaronski, 2007; 2010; Meyling and Eilenberg, 2007).

1083 Fungi have many desirable traits that favor their development as biological control agents.
1084 They pose minimal risk to beneficial non-target organisms such as bees, earthworms and
1085 Collembola, which are key ecosystem service-providers, and arthropod natural enemies such as
1086 parasitic wasps and predatory beetles (Goettel et al., 2001; Traugott et al., 2005; Brownbridge
1087 and Glare 2007; O'Callaghan and Brownbridge, 2008). This enhances their potential role in
1088 IPM; the preservation of natural enemies allows them to make a greater contribution to the
1089 overall regulation of pests, and maintenance of biodiversity is increasingly recognized as being
1090 critical to the long-term productivity of our farms and forests. Their newly found attributes also
1091 provide the possibility of their use in multiple roles, for instance in addition to arthropod pest
1092 control, simultaneous suppression of plant pathogens and plant parasitic nematodes (Goettel et
1093 al., 2008; Kim et al., 2009; Koike et al., 2011) or biofertilizers (Kabaluk and Ericsson, 2007;
1094 Behie et al., 2012).

1095 Chandler et al. (2008) considered the development of anamorphic fungi, e.g., *B. bassiana*, *M.*
1096 *anisopliae*, to have followed an 'industrial' pathway; mass-production systems have been
1097 devised to provide large quantities of inoculum which can then be formulated and repeatedly

1098 applied as sprays, granules, etc. (Shah and Pell, 2003; Brownbridge, 2006; Charnley and Collins,
1099 2007). Conversely, pest control strategies using entomophthoralean fungi have relied more on
1100 ‘ecological’ approaches; accompanying research has focused on understanding conditions that
1101 promote natural epizootics, e.g. manipulating environmental conditions to enhance disease
1102 incidence and spread, use of inoculative releases to establish the disease within a pest population
1103 to achieve long-term suppression, or conservation of natural epizootics (Steinkraus et al., 2002;
1104 Steinkraus, 2006, 2007; Nielsen et al., 2007; Pell, 2007; Hajek, 2009; Solter and Hajek, 2009;
1105 Pell et al., 2010).

1106 Commercial products based on some of the pathogenic fungi – mycoinsecticides and
1107 mycoacaricides – are primarily based on *Beauveria spp.*, *Metarhizium spp.*, *Isaria fumosorosea*
1108 (formerly *Paecilomyces fumosoroseus*), and *Lecanicillium spp.* (Inglis et al., 2001; Faria and
1109 Wraight, 2007; Wraight et al., 2007; Alves et al., 2008). Table 3 provides examples of fungi used
1110 for the microbial control of several insect and mite pests. Fungal products largely occupy niche
1111 markets, often within individual countries or geographically linked regions. In most cases, fungi
1112 are actively applied as microbial pesticides to regulate pest populations, and pathways towards
1113 their development and regulation have generally mirrored those of synthetic pesticides. Despite
1114 these positive developments, fungi remain an under-utilized resource for pest management. How
1115 far has the field progressed since Lacey et al.’s 2001 publication to move us closer to realizing
1116 this biological control potential? Here, we will highlight some of the recent developments that
1117 may promote opportunities to use entomopathogenic fungi and identify some of the critical
1118 factors that still need to be addressed to enable their wider utilization.

1119

1120 **4.2 Mode of action**

1121 All fungi have the same basic mode of action. Excellent reviews of the mechanical, molecular
1122 and biochemical processes involved in insect infection are available and consequently will not be
1123 covered here in detail (*e.g.*, *see* Hajek and St. Leger, 1994; Hajek, 1997; Inglis et al., 2001;
1124 Charnley, 2003; Charnley and Collins, 2007; Ortiz-Urquiza and Keyhani, 2013). Insect control
1125 by entomopathogenic fungi is achieved when sufficient infective propagules (generally conidia)
1126 contact a susceptible host and conditions are suitable for a lethal mycosis to develop. Fungi have
1127 been applied for soil pest control by direct incorporation of conidia, mycelial pellets,
1128 microslerotia or inert or nutrient-based granules containing fungal propagules (conidia or
1129 mycelia) (Brownbridge, 2006; Charnley and Collins, 2007; Jaronski, 2007; Ansari et al., 2008;
1130 Jaronski and Jackson, 2008), whereas foliar-feeding pests have typically been targeted by sprays
1131 of formulated conidia (Jaronski, 2010).

1132 Fungal isolate virulence towards different arthropod hosts varies. Virulence generally
1133 decreases with repeated sub-culture on artificial media, and can often be regained through host
1134 passage (*e.g.* Nahar et al., 2008). Virulent isolates generally express an abundance of spore-
1135 bound proteases, efficiently produce and release exoenzymes during cuticular penetration, and
1136 generate toxins as the fungus colonizes the host (Vey et al., 2001; Freimoser et al., 2005; Shah et
1137 al., 2005; Qazi and Khachatourians, 2007; Zimmermann 2007a; 2007b; 2008; Khan et al., 2012).
1138 Selecting superior strains exhibiting these characteristics, or manipulating isolates to promote
1139 these traits, has been seen as a way of overcoming what is often considered a significant
1140 impediment to their wider use, *i.e.*, fungi kill their hosts too slowly. Fungal virulence can also be
1141 improved through directed genetic manipulation whereby specific genes are inserted into the
1142 fungal genome to promote expression of toxins that increase the virulence of the parent
1143 organisms, *e.g.*, insertion of scorpion toxin genes into *M. anisopliae* and *B. bassiana* (Wang and

1144 St. Leger, 2007; Pava-Ripoll et al., 2008; St Leger et al, 2011). In both cases, the recombinant
1145 strains exhibited dramatically increased virulence. This approach has the potential to improve
1146 insect kill and reduce the amount of inoculum needed to regulate a pest population. In addition,
1147 protoplast fusion can be used to enhance virulence and increase host range. For instance,
1148 protoplast fusion was used with several strains and species of *Lecanicillium* to develop hybrid
1149 strains with multiple effects (toxic and parasitic) against plant parasitic nematodes, plant
1150 pathogens and aphids, with plant competency (as root colonizers and endophytes), making these
1151 strains promising for development as broad-spectrum microbial pesticides targeting plant
1152 pathogens, insects, and plant parasitic nematodes (Goettel et al., 2008; Koike et al, 2011).

1153 Entomophthoralean fungi actively eject spores when conditions are favorable (high
1154 humidity) that can rapidly infect a susceptible insect, even when these conditions only prevail for
1155 short periods (Steinkraus, 2006). This trait gives these pathogens great epizootic potential, and in
1156 many groups of insects, they are among the most important natural mortality factors. In contrast,
1157 spores of the hypocrealean fungi *Beauveria* and *Metarhizium* spp. tend to be dispersed passively,
1158 via wind currents or rain splash, although transmission can also occur when susceptible insects
1159 contact infected individuals, or conidia can be distributed on the bodies of other arthropods
1160 (Rath, 2002; Wraight and Ramos, 2002; Meyling and Eilenberg, 2006b; Meyling et al., 2006;
1161 Roy et al., 2007; Vega et al., 2007). Both hypocrealean and entomphthoralean fungi can survive
1162 repeated intervals of low humidity, recommencing development (infection) when favorable
1163 conditions return. This can result in spectacular epizootics such as those observed in whitefly
1164 infestations on cotton when the canopy closes and creates a humid microclimate that favors host
1165 infection and spread of the disease within the population (Lacey et al., 1996). These fungi can,
1166 though, infect insects even under conditions of low ambient humidity; attachment of the small

1167 conidia at infection sites within inter-segmental folds or under elytra where humidity levels are
1168 high may account for this, and the localized microclimate that exists around an insect or at the
1169 insect-leaf interface may have a more significant impact on the infection process than ambient
1170 conditions (Inglis et al., 2001; Vidal et al., 2003; Vidal and Fargues, 2007; Jaronski, 2010).

1171 Fungi can persist in the soil for several years with new ‘flushes’ of inoculum provided
1172 following the successful infection and colonization of a susceptible host. This leads to localized
1173 high concentrations of infective conidia and greater opportunities for insect infection to occur
1174 (Enkerli et al., 2001; Rath, 2002; Milner et al., 2003; Keller et al., 2003; Meyling and Eilenberg,
1175 2007). Long-term survival of entomopathogenic fungi within an environment appeared to be
1176 reliant upon access to susceptible hosts, though, as they were generally considered weak
1177 saprophytes (Keller et al., 2003; Hummel et al., 2002; Roberts and St. Leger, 2004; Jaronski,
1178 2007). However, the recent discoveries of their roles as endophytes or rhizosphere competent
1179 organisms require further investigations in this regard. For those species with relatively narrow
1180 host-spectra, lack of hosts can limit their natural occurrence and longevity (Keller et al., 2003;
1181 Meyling and Eilenberg, 2007).

1182

1183 ***4.3 The changing face of fungi***

1184 A variety of molecular tools and systems now augment more traditional fungal classification
1185 schemes, allowing examination of evolutionary (phylogenetic) relationships between isolates as
1186 well as matching anamorphs and teleomorphs (Driver et al., 2000; Rehner and Buckley, 2005;
1187 Hibbett et al., 2007; Humber, 2008; Bischoff et al, 2009; Blackwell, 2010). Furthermore, they
1188 aid in the differentiation and identification of fungi in environmental samples, enable definition
1189 of potential associations (habitat, host), and may provide valuable insights that enable strain

1190 improvements or selection of isolates with specific traits (Nielsen et al., 2001; Ranjard et al.,
1191 2001; Sung et al., 2001; Bidochka et al., 2002; Enkerli et al., 2005; Huang et al., 2005; McGuire
1192 et al., 2006; Nielsen et al., 2005; Rehner et al., 2006; Hibbett et al., 2007; Inglis et al., 2007;
1193 Sung et al., 2007; Meyling et al., 2009; Enkerli and Widmer, 2010). These techniques are
1194 changing the way we observe fungi in the environment, and potentially alter pathways towards
1195 their development as MCAs.

1196

1197 ***4.4 The importance of selecting the appropriate fungal isolate and other considerations***

1198 The literature is replete with examples of fungi that have performed well in laboratory trials and
1199 shown “great potential” (Vega et al., 2012) only to fail once they were tested in the field. This
1200 has often led to a search for ‘new and better’ isolates rather than investigating underlying factors
1201 impacting performance in the environment. Without diminishing the implicit value of looking for
1202 new organisms (in general there is no shortage of excellent candidates) more research emphasis
1203 is instead needed to address critical factors to turn ‘potential’ into viable ‘product’.

1204 Isolates must be ecologically competent to function and persist in the environment of the
1205 target pest, and selection of candidates must not be solely based on performance in an optimized
1206 bioassay system. Bioassays need to be carried out under discriminatory conditions that attempt to
1207 replicate conditions where the pathogen will be used (Butt and Goettel, 2000). Environmental
1208 and insect behavioral factors all influence pathogen activity, so their incorporation into a testing
1209 scheme will enable robust isolates to be identified prior to downstream development activities.

1210 Fungi and arthropods have evolved complex relationships, and some soil-dwelling
1211 arthropods show adaptive behavioral responses that prevent their coming into contact with fungal
1212 inoculum (Villani et al., 2002; Thompson and Brandenburg, 2005; Baverstock et al. 2010). There

1213 also appears to be variation in the level of response to different fungal isolates or fungal growth
1214 stages, i.e. vegetative stage vs conidia (Thompson and Brandenburg, 2005), and in some
1215 instances, insects may be attracted or repelled by fungal volatiles or metabolites which could
1216 enhance or deter activity (Villani et al., 1994; Engler and Gold, 2004; Kepler and Bruck, 2006;
1217 Meyling and Pell, 2006c; Rohlf and Churchill, 2011). Such behavioral responses should be
1218 taken into consideration when selecting appropriate strains for insect pest management, and the
1219 type of inoculum used in a pest management program. Similarly, our ability to manipulate insect
1220 behavior through the use of a variety of compounds may provide new opportunities to enhance
1221 pathogen efficacy (Roy et al., 2007).

1222

1223 ***4.5. Ecological considerations***

1224 Entomopathogenic fungi are natural components of most terrestrial ecosystems. . Greater
1225 understanding of the fundamental ecology of these organisms in the natural environment and
1226 post-application would be of immense value in the development of more ecologically sound
1227 control approaches (Wraight and Hajek, 2009; Vega et al., 2009; Roy et al, 2010a, 2010b). The
1228 lack of field data is due, in part, to the complexity of the environment and the intricate
1229 interactions between different environmental and biological factors that can confound
1230 observations around cause and effect (Jaronski, 2007). Likewise, interactions among biotic and
1231 abiotic factors, e.g., sunlight, humidity, and microbial activity on the phylloplane, affect efficacy
1232 and persistence of fungal treatments applied against foliar pests (Jaronski, 2010). While in vitro
1233 testing can provide valuable insights into fungal responses to specific inputs, they rarely yield
1234 data that can be directly extrapolated to predict field responses. More effort needs to be invested
1235 in the evaluation of effects of agricultural practices (e.g., Klingen et al., 2002a; 2002b; Hummel

1236 et al., 2002; Townsend et al., 2003) on persistence and particularly efficacy under field
1237 conditions.

1238 Production of good ecological data has also been impeded by a historic lack of tools to
1239 examine and quantify fungal populations. Traditionally, studies have relied on time-consuming
1240 isolation and plating techniques. Similarly, risk assessments have tended to focus on interactions
1241 with macroorganisms; monitoring of interactions with other microbes has been limited and
1242 biased by our inability to culture all soil and foliar microorganisms. However, new tools and
1243 increasingly powerful molecular methods are becoming available to examine fungal
1244 communities and may be applied to the study of entomopathogens. For example, use of nuclear
1245 ITS and EF1-alpha sequences have enabled isolates to be differentiated and phylogenetic
1246 relationships within species to be determined, enabling links to geographic and host origins to be
1247 defined (Driver et al., 2000; Bidochka et al., 2001; 2002; Rehner and Buckley, 2005; Rehner et
1248 al., 2006; Inglis et al., 2008; Meyling et al., 2009; Inglis et al., 2012). The ability to transform
1249 fungi to express the green fluorescent protein (GFP) allows GFP-mutants to be observed in-situ,
1250 and expression of the protein may be tied to specific events during infection or growth through
1251 choice of an appropriate promoter (Lorang et al., 2001; Hu and St. Leger, 2002; Skadsen and
1252 Hohn, 2004; Wu et al., 2008). A variety of other molecular techniques such as RFLP, T-RFLP,
1253 AFLP and strain-specific microsatellite markers have been used as diagnostic tools allowing
1254 fungi to be tracked in the environment (Enkerli et al., 2001; 2004; 2005; Castrillo et al, 2003;
1255 Rehner and Buckley, 2003; Schwarzenbach et al., 2007a, 2007b; Inglis et al., 2008; Enkerli and
1256 Widmer, 2010; Inglis et al., 2012). Advances in the use of PCR techniques provide highly
1257 specific methods of monitoring fungal populations in 'real time' and in a quantitative manner, in
1258 soils, insects, and in plants (Ownley et al., 2004; Wang et al., 2004; Entz et al., 2005; Castillo et

1259 al., 2008; Meyling et al., 2009; Enkerli and Widmer, 2010; Inglis et al., 2012). Use of qPCR with
1260 automated ribosomal intergenic spacer analysis (ARISA) allow soil microbial communities to be
1261 profiled and responses to specific events to be monitored; these techniques are likely to be
1262 increasingly applied to the study of entomopathogens to assess the fate of biological control
1263 species and their impacts on microbial community structure (Ranjard et al., 2001; Hartmann et
1264 al., 2005; Shah et al., 2009; Torzilli et al., 2006; Martin, 2007; Enkerli, 2008; Enkerli and
1265 Widmer, 2010; Inglis et al., 2012).

1266 All biotic factors in soils are influenced by prevailing environmental conditions, soil types,
1267 nutrient status, agricultural practices and inputs in the form of pesticides and soil amendments.
1268 Intricate interactions between abiotic and biotic factors make it extremely difficult to quantify
1269 the specific effects of each of these on the dynamics of entomopathogenic fungi in soil (e.g.
1270 Quesada-Moraga et al., 2007). However, we can identify three principle biotic components that
1271 have a major influence on fungal persistence and efficacy. These are: soil microorganisms,
1272 plants, and invertebrates.

1273 Generally speaking, entomopathogenic fungi are considered weak saprophytes in the
1274 competitive soil environment, and introduced inoculum levels will decline in the absence of an
1275 arthropod host (Inglis et al., 2001; Roberts and St. Leger, 2004; Längle et al., 2005). Metabolites
1276 produced by other soil microbes can adversely affect germination and growth, or be directly
1277 toxic, leading to reduced infectivity or multiplication; consequently, survival and efficacy of
1278 entomopathogens is commonly superior in sterilized vs non-sterilized soils (Jaronski, 2007).
1279 Even so, in native soils conidia will infect a susceptible host when they contact the insect cuticle;
1280 *Metarhizium* and *Beauveria* will germinate, grow, and conidiate when applied to soil and
1281 amendment of soil with nutrients can overcome (apparent) fungistasis (Keller, 2000; Milner et

1282 al., 2003; Bruck, 2005; Chandler and Davidson, 2005; Brownbridge, 2006; Jaronski, 2007;
1283 Jaronski and Jackson, 2008). This suggests that fungistasis alone is not the sole reason for the
1284 low germination in soil and fungi may require additional host- or nutrient-derived cues to initiate
1285 development. Antibiosis also occurs between entomopathogenic fungi and other
1286 microorganisms, a phenomenon that has implications for protection of crop plants from
1287 pathogens (Ownley et al., 2004; 2010). Very few attempts have been made to evaluate effects of
1288 phylloplane microorganisms on persistence and infectivity of fungi applied to foliage, in spite of
1289 the fact that plant surfaces are occupied by a diverse range of microfauna (Jaronski, 2010).

1290 Crop plant species and tillage practices affect the prevalence and persistence of fungi
1291 (Hummel et al., 2002; Klingen et al., 2002b; Jaronski, 2007). Fungal entomopathogens could be
1292 affected by plant surface chemistry and volatiles (Cory and Ericsson, 2010). Some
1293 entomopathogens, particularly *M. anisopliae*, are more commonly associated with agricultural
1294 (tilled) soils than natural habitats, although fungal prevalence and diversity is normally greater in
1295 undisturbed soils (Bidochka et al. 2001; 2002; Inglis et al., 2008; Meyling and Eilenberg, 2007;
1296 Meyling et al., 2009). Plant root exudates contain many nutrients that support the development of
1297 microbial populations in the rhizosphere; in vitro tests demonstrated that carbohydrates and
1298 nitrogen compounds stimulate germination and growth of *M. anisopliae* conidia, while organic
1299 acids may inhibit germination (Li and Holdom, 1995). Some *M. anisopliae* isolates are
1300 rhizosphere-competent, a trait that enhances persistence in the root zone (Hu and St. Leger,
1301 2002; Bruck, 2005; St. Leger, 2008). The physiological adaptation of the fungus to function as a
1302 pathogen or saprophyte involves expression of different gene products, demonstrating that the
1303 fungus appears to have evolved various mechanisms that enhance survival in different

1304 environments (Wang et al., 2005; Wang and St. Leger, 2007; Bruck, 2010; St. Leger et al.,
1305 2011).

1306 Endophytes may be broadly defined as microbes that live in healthy plant tissue (Hyde and
1307 Soyong, 2008). Commonly, these are bacteria and fungi that have either no effect or have a
1308 beneficial relationship with their host, including the ability to naturally confer resistance to pests
1309 and diseases (Backman and Sikora, 2008). Recently, *B. bassiana* has been recognized as an
1310 endophyte that occurs naturally in, or has been successfully introduced into a diverse range of
1311 plant species (Vega et al., 2008; Parsa et al., 2013). In several instances, colonization of plant
1312 tissues by the fungus has provided protection against insect damage or has inhibited insect
1313 development and establishment, such as the banana weevil, *Cosmoplites sordidus* (Akello et al.,
1314 2008), stem borer, *Sesamia calamistis* (Cherry et al., 2004), and the cynipid, *Iraella luteipes*
1315 (Quesada-Moraga et al., 2009), probably as a result of *in planta* production of insecticidal
1316 metabolites by triggering host-plant defenses, or as a result of feeding deterrence/antibiosis.
1317 Some isolates have also demonstrated anti-microbial activity and can provide protection against
1318 infection by plant pathogens (Ownley et al., 2004; 2010) including most recently, the zucchini
1319 yellow mosaic virus in cucurbits (Jaber et al., 2014). As endophytes, the fungi are in a protected
1320 environment where they are not exposed to abiotic and biotic factors that can limit efficacy when
1321 fungi are applied to foliage or the soil, and may offer protection against cryptic species, e.g.,
1322 stem borers, that would otherwise be difficult to control (Brownbridge, 2006; Jaronski, 2007,
1323 2010).

1324 Foliar topography and chemistry can affect fungal activity and persistence (Jaronski, 2010).
1325 While the specific physical traits or compounds responsible for these observed differences are
1326 often unknown, the work of several authors indicate that both factors can significantly impact

1327 insect infection due to reduced rates of conidial acquisition (Kouassi et al., 2003; Ugine et al.,
1328 2007) and the toxic effects of chemicals produced (as exudates or volatiles) at the leaf surface
1329 (Inyang et al., 1998) or consumed by the host (Olleka et al., 2009). Efficacy may be further
1330 compromised by the use of inefficient application practices and different spray parameters on
1331 crops at different stages of development, which has been clearly shown to affect insect infection
1332 rates (Ugine et al., 2007). Clearly, we need to develop a better understanding of the complex
1333 interactions between a range of factors, e.g., crop type and physiology, age, fungal strain, pest
1334 biology, method of application, etc., to devise efficient use practices.

1335 Invertebrates have many effects on entomopathogen levels in soil. Some, such as
1336 Collembola, mites and earthworms, ingest conidia and play a role in their dispersion within and
1337 removal from soil (Broza et al., 2001; Dromph, 2003; Milner et al., 2003; Brownbridge and
1338 Glare, 2007; Shapiro-Ilan and Brown, 2013). Insect hosts are critical to the long-term survival of
1339 many species of entomopathogenic fungi. Access to and successful infection of a host is the only
1340 way in which some species can significantly multiply. Fungal prevalence over time may thus be
1341 closely correlated with the presence of susceptible insect populations (Meyling and Eilenberg,
1342 2007), although the extent that they reproduce endophytically or epiphytically remains to be
1343 determined. Use of insecticides may contribute to the decline of fungal populations by reducing
1344 the availability of suitable hosts rather than having direct negative effects on fungal survival
1345 (Klingen and Haukeland, 2006). Unfortunately, most studies on effects of chemical pesticides on
1346 viability of entomopathogenic fungi have been carried out using *in vitro* techniques that bear
1347 little resemblance to the agricultural system in which the pathogen will encounter the chemical.
1348 This is an area of research that could be highly beneficial. Knowledge of positive or negative
1349 interactions could allow IPM practices to be adjusted to favor insect infection.

1350 An avoidance response to conidia of both *M. anisopliae* and *B. bassiana* has been observed
1351 in mole crickets, which may lead to inconsistent performance of these fungi in the field (Villani
1352 et al., 2002; Thompson and Brandenburg, 2005). However, there appears to be variation in the
1353 level of response to different isolates (Thompson and Brandenburg, 2005). Insects may also be
1354 attracted to fungi. Engler and Gold (2004) showed that termites were attracted to mycelial
1355 preparations and volatile extracts of *M. anisopliae*, and *P. japonica* females preferentially
1356 oviposited in soils treated with mycelia (Villani et al., 1994). This recruitment effect was also
1357 seen with black vine weevil (BVW) *Otiiorhynchus sulcatus* larvae, which responded positively to
1358 *M. anisopliae*-treated media (Kepler and Bruck, 2006). Such behavioral responses should be
1359 taken into consideration when selecting appropriate strains for insect pest management and may
1360 be useful in the development of more effective biological control strategies.

1361

1362 **4.6 Production and formulation**

1363 Following the traditional model, mass production systems have been devised to maximize
1364 inoculum yield at the lowest possible cost for use in inundative applications (Wraight et al.,
1365 2001; Cliquet and Jackson, 2005; Jackson et al., 2010; Jaronski, 2010; Jaronski and Jackson,
1366 2012). Research emphasis has been placed on optimization of biomass production, stability, and
1367 ease of handling for application (Charnley and Collins, 2007). The general assumption has been
1368 that control could be achieved if sufficient inoculum could be produced cheaply enough and
1369 applied at sufficiently high rates (Brownbridge et al., 2008; Jaronski, 2010). The role of the
1370 environment and its impact on fungal activity has not necessarily been a primary consideration
1371 driving the development of production and formulation techniques (Jackson et al., 2010).
1372 However, there is considerable scope to modify production media and techniques to provide

1373 more ecologically competent infective material that is better suited to use in specific
1374 environments. Greater knowledge of prevailing ecological factors in the pest's habitat will allow
1375 potential constraints to fungal survival and/or infection to be identified, and will provide leads
1376 for research to overcome these constraints. When combined with development of alternative
1377 delivery mechanisms, it is likely that more efficacious microbial control products will become
1378 available.

1379 Efficacy against soil-inhabiting pests is influenced by many biotic and abiotic factors.
1380 Consequently environmental factors are critical to performance, and maintenance of bioactivity
1381 must be a primary consideration when developing production media (Kiewnick, 2004; Tarocco
1382 et al., 2005; Brownbridge, 2006; Jaronski, 2007, 2010). Formulation can enhance characteristics
1383 or render fungal preparations easier to apply, but their performance is ultimately reliant upon
1384 inclusion of robust biological material that is "fit for purpose" (Jackson, 1999; Brownbridge et
1385 al., 2008). The production method selected will depend upon the nature of the inoculum required,
1386 and isolates may have different growth characteristics on different production media (Shah et al.,
1387 2005; Charnley and Collins, 2007; Jaronski and Jackson, 2012). An excellent overview of
1388 ecological considerations in the production and formulation of entomopathogenic fungi was
1389 recently published by Jackson et al. (2010), and readers are referred to it for a more complete
1390 review of these factors.

1391 Solid substrates have been widely used to produce aerial conidia of entomopathogenic and
1392 other beneficial fungi (Kiewnick, 2001; Wraight et al., 2001; Krishna, 2005; Charnley and
1393 Collins, 2007; Jaronski and Jackson, 2012). Temperature, pH, aeration and substrate components
1394 all influence conidial yield, viability, stability and virulence (Jaffee and Zasoski, 2001; Shah and
1395 Butt, 2005; Shah et al., 2005; Rangel, 2006; Jackson et al., 2010). Although these parameters are

1396 more difficult to regulate in a solid-substrate system, this remains the predominant method used
1397 for commercial products due, in part, to the flexibility of a system that lends itself to the cottage-
1398 industry production scale used in many parts of the world. Solid-state fermentation bioreactors
1399 yielding up to 3×10^{13} conidia per kg of substrate have been developed (Jenkins and Gryzwacz,
1400 2000; Wraight et al., 2001; Kiewnick, 2004; Kang et al., 2005; Kiewnick and Sikora, 2006;
1401 Jaronski and Jackson, 2012).

1402 The economies of large-scale liquid fermentation processes for microorganisms is well
1403 established and has provided the paradigm for the mass production of microbes with
1404 pharmaceutical (e.g., production of insulin) or nutraceutical (e.g., probiotics) applications. Large-
1405 scale liquid fermentation systems are successfully used for agriculturally important bacteria (e.g.,
1406 *B. thuringiensis*, *S. entomophila*). In submerged culture, fungi generally produce vegetative
1407 propagules – mycelia or yeast-like blastospores; culture conditions and media composition will
1408 have a primary influence on the type and amount of inoculum produced (Jackson et al., 2003;
1409 Vega et al., 2003; Cliquet and Jackson, 2005; Charnley and Collins, 2007; Jaronski and Jackson,
1410 2012). Production systems have been designed with high yield as a primary goal but again, the
1411 infectivity of the resulting biomass and its ecological competence and stability are key factors
1412 that must be considered during process development. Culture conditions and media can be
1413 manipulated to impart specific traits to the resulting biomass, including enhanced infectivity
1414 (potency) and stability during drying and in storage (Vega et al., 2003; Cliquet and Jackson,
1415 2005; Liu and Chen, 2005; Leland et al., 2005a; 2005b; Jackson et al., 2006; Jaronski and
1416 Jackson, 2008; 2012). Jaronski and Jackson (2008; 2012) and Jackson et al. (2010) recently
1417 described methods to induce production of microsclerotia by *M. anisopliae* in liquid media. The
1418 aggregates were readily air-dried, stable at room temperature, and showed superior efficacy

1419 against sugarbeet root maggot in soil assays compared with conventional corn-grit granules. The
1420 material sporulated profusely in non-sterile soils and was active at low soil moisture levels
1421 (Jaronski, 2007; Jaronski and Jackson, 2008). Such production/formulation techniques overcome
1422 some of the biotic and abiotic constraints to fungal efficacy and may increase opportunities to
1423 utilize these biocontrol agents against soil pests.

1424 Advances in formulation technologies now permit stabilization of environmentally sensitive
1425 microbes and have applications to a diverse variety of beneficial organisms. Formulations can
1426 improve the handling characteristics and safety of a microorganism (e.g., by eliminating spore
1427 dust during preparation of a spray mixture), enhance stability pre- and post-application, improve
1428 persistence, promote efficacy, and facilitate easy delivery to the target pest (Wraight et al., 2001;
1429 Brownbridge, 2006; Brownbridge et al., 2006; Jackson et al., 2006; Thompson et al., 2006;
1430 Charnley and Collins, 2007; Jaronski, 2007; 2010; Jaronski and Jackson, 2008; Jackson et al.,
1431 2010). Critical, however, is maintenance of viability, ideally even when storage conditions are
1432 sub-optimal (Jackson et al., 2010). Effective formulation is integral to the wider utility of
1433 microbial pesticides in agricultural production systems, and microbes can fail if formulated
1434 poorly. Formulations may be tailored to suit the environment in which the microbial will be
1435 used, the delivery system envisioned, and the nature of the inoculum being used. Like production
1436 systems, they must be rationally developed to ensure retention of key characteristics that are
1437 critical to microbial efficacy, in both foliar and soil environments (Jaronski, 2010). For example,
1438 an oil formulation of *M. anisopliae* var. *acidum* was developed to overcome the limitations of
1439 dry habitats for the control of locusts and grasshoppers (Lomer et al., 1999, 2001; Bateman,
1440 2004; Moore, 2008).

1441

1442 **4.7 Improving delivery**

1443 While mass production systems can be refined to overcome particular environmental constraints,
1444 strategies for more efficient use also need to be investigated to capture the full potential of these
1445 microbes, as well as to reduce the amount of inoculum required to achieve satisfactory control
1446 because there is a physical and economical limit to the amount of material that can be applied.
1447 Some circumstances may require repeated pesticidal application of fungal biocontrol agents
1448 where simple sprays are not appropriate or effective. Control of cryptic insects, for example,
1449 cannot be achieved using conventional sprays. We thus need to look to application techniques
1450 that are not only more efficient, but use less material. As with other development criteria,
1451 consideration of the pest's biology is paramount to devising novel delivery techniques.

1452 The pollen beetle *Meligethes aeneus*, is a widespread pest of oilseed rape and other important
1453 cruciferous crops in Europe. Adults and larvae feed on pollen in buds and open flowers, affecting
1454 seed set and hence yield. The beetles are very difficult to reach with regular sprays in this
1455 protected environment. Honey-bees (*Apis mellifera*), frequent visitors to oilseed crop flowers to
1456 forage for nectar and pollen, were successfully used to vector dry *M. anisopliae* conidia to
1457 flowers of oilseed rape, leading to subsequent high levels of pollen beetle mortality and mycosis
1458 (Butt et al., 1998). Honey bees have subsequently been used to disseminate *B. bassiana* to canola
1459 flowers for control of tarnished plant bug, *Lygus lineolaris* (Al-mazra'awi et al., 2006a) and can
1460 vector dry conidia to a range of agriculturally important crops, demonstrating additional
1461 opportunities to use bees to deliver these control agents (Al-mazra'awi et al., 2007). Bumble bees
1462 are used to pollinate many greenhouse crops, and can also be employed to vector *B. bassiana* and
1463 other microbial inoculants to control thrips, tarnished plant bug and grey mold in greenhouse
1464 tomato and sweet pepper (Al-mazra'awi et al., 2006b). In all cases, fungal delivery was

1465 efficiently targeted to the portion of a crop where pest damage was occurring, and relatively
1466 small amounts of conidia were needed to effect control (Kapongo et al. 2008 a, 2008 b; Kevan et
1467 al., 2008).

1468 Fungi can be delivered into the soil environment via seed coatings. This technique has
1469 traditionally been used to protect seeds and developing seedlings from soil-borne diseases and
1470 subterranean pests with persistent broad-spectrum fungicides and insecticides. With the advent of
1471 new polymers that can be used to coat materials onto seeds without heat, seed-coating with
1472 microbes has become possible. Seed coating with fungal inoculants can be used to establish
1473 fungi such as *Trichoderma* spp. in the rhizosphere and prevent losses to root diseases. Rhizo-
1474 competent entomopathogens such as *M. anisopliae* may establish on the developing roots of
1475 seedlings, mitigating insect damage, and endophytic entomopathogens such as *B. bassiana* may
1476 colonize the plant providing resistance to plant pathogens. Although the biological control
1477 effectiveness of these approaches needs to be validated, targeted suppression of a pest with
1478 reduced amounts of inoculum could be provided.

1479 Efficiencies may also be realized using auto-dissemination devices. Several insect pests have
1480 been effectively regulated using this approach (Vega et al., 2007; Baverstock et al., 2010). Tsetse
1481 flies, *Glossina* spp., are major impediments to rural development in many African countries.
1482 Previous control attempts have focused on habitat manipulation and widespread application of
1483 insecticides. The long-term efficacy of these approaches is poor and the high cost and
1484 environmental risks posed by widespread insecticide applications have provided the impetus to
1485 develop alternative management approaches. Area-wide spray applications of fungi are
1486 impractical due to issues of cost, targeting, and poor field persistence, creating an ideal scenario
1487 for development of an auto-inoculation device. Various traps have been devised that are highly

1488 attractive to tsetse, e.g., bi-conical traps baited with cow urine (Dransfield et al., 1990); by
1489 combining this technology with an inexpensive trap-and-release inoculation device, an efficient
1490 and economical method of delivering lethal doses of *M. anisopliae* conidia to adult tsetse was
1491 developed in Kenya (Maniania et al., 2002). A similar approach was taken to the development of
1492 an auto-dissemination device for control of adult fruit flies (Dimbi et al., 2003; Ekesi et al.,
1493 2007). The potential for horizontal transmission among inoculated individuals further enhances
1494 the likelihood that these pests can be controlled using fungi in an auto-inoculation device
1495 (Quesada-Moraga et al., 2008; Thaochan and Ngampongsai, 2015).

1496 Auto-dissemination devices show promise for use against pests of field vegetable and fruit
1497 crops, and in forested areas, where widespread conventional applications of fungal pathogens are
1498 impractical. A common behavioral phenomenon among many beetles is that they overwinter *en-*
1499 *masse*, providing opportunities to target a fungal treatment to a compact population (Dowd and
1500 Vega, 2003). Overwintering sap beetles, *Carpophilus luqubris*, were contaminated and infected
1501 with a virulent strain of *B. bassiana* using an auto-inoculative device baited with pheromones.
1502 Insects were targeted as they left harvested cornfields in the fall; the disease spread within the
1503 population by horizontal transmission and established in the overwintering population (Dowd
1504 and Vega, 2003). Autoinoculative devices were also successfully used to introduce *B. bassiana*
1505 into a population of spruce bark beetle, *Ips typographus* (Kreutz et al., 2004). Transmission of
1506 the pathogen occurred between treated and non-treated individuals and significantly reduced
1507 adult beetle damage to spruce trees and numbers of beetle larvae under spruce bark. The capacity
1508 to control other insects of agricultural importance using this technology has been reviewed by
1509 Vega et al. (2007). This includes pests with cryptic habits such as leafminers, which are very
1510 difficult to control with microbial or conventional pesticides (Migiro et al., 2010). Knowledge of

1511 pest biology is essential to the development of these novel yet simple technologies, which have
1512 excellent potential to provide selective and cost-efficient means of control.

1513 Insect behavior may be manipulated with a variety of allelochemicals and other compounds
1514 in ways that may improve the efficiency of pathogen-based pest control strategies (Pell et al.,
1515 2007; Baverstock et al., 2010). For example, a variety of thrips allelochemicals will attract, arrest
1516 or repel these insects, raising the possibility of using these materials to concentrate thrips into
1517 specific areas of a crop (Tsao et al., 2005; Teulon et al., 2007a, 2007b; Davidson et al., 2007;
1518 2008). Use of attractants with repellent compounds allows us to consider development of a
1519 “push-pull” approach in greenhouse crops (van Tol et al., 2007). By concentrating infestations in
1520 a limited area, control efforts can be focused there, rather than blanket-spraying an entire crop.

1521 The differential attraction of some insect pests to particular plant varieties or species offers
1522 another way in which pest behavior can be modified to enhance the efficacy of fungal biocontrol
1523 agents. For example, western flower thrips are more strongly attracted to some varieties of
1524 chrysanthemum, which can be used as ‘trap plants’ within a production system (Buitenhuis and
1525 Shipp, 2006). Trap plants can be arranged as “islands” within a crop and fungal biocontrol agents
1526 applied to the islands within a wider cropping area. Despite a wide host range, the black vine
1527 weevil has distinct preferences for feeding and oviposition. Adults are differentially attracted to
1528 plant volatiles (van Tol et al., 2002), and insect feeding damage on *Taxus* and *Euonymus* spp.
1529 invokes the production of odors that are highly attractive to other beetles (van Tol et al., 2002;
1530 2004). These and other attractive plants can be used as trap crops to limit weevil distribution and
1531 egg-laying to specific areas, allowing control efforts such as *M. anisopliae* (Bruck, 2005; Shah et
1532 al., 2007) to be focused on the trap plants. Furthermore, some fungi appear to attract the weevils,

1533 which may further improve efficacy (Kepler and Bruck, 2006). By defining more efficient use
1534 practices for insect pathogens, such controls become more cost-effective.

1535 Synergistic interactions have often been observed when fungal pathogens have been co-
1536 applied with sub-lethal doses of insecticides. Synergism is thought to occur due to the action of
1537 the insecticide on the insect's behavior, either stimulating movement through treated media in an
1538 attempt to escape to a less toxic environment and, in the process, leading to the acquisition of
1539 more fungal inoculum, or adversely affecting movement and grooming behavior, leading to
1540 greater retention of inoculum on the body of an insect (Quintela and McCoy, 1998; Jaramillo et
1541 al., 2005; Shah et al., 2007; 2008; Ansari et al., 2007). Synergism leading to improved efficacy
1542 and control may also occur when different species or strains of fungi are applied concurrently.
1543 For example, combined application of *B. bassiana* and *M. acridum* (identified as *M. flavoviride*)
1544 could be used to overcome some of the constraints of temperature in thermoregulating pests such
1545 as grasshoppers, especially where temperatures fluctuate or are high for a significant period of
1546 time (Inglis et al., 1997). Application of entomopathogenic fungi can also be practiced in
1547 combination with other insect pathogens, including nematodes and Bt (Ansari et al., 2008; 2010;
1548 Wraight et al., 2009). Combined applications may render the insect host more susceptible by way
1549 of compromising health, prolonging developmental stages, or simply by the combined action of
1550 two microbes on different components of the pest population. Similar effects can be obtained by
1551 using entomopathogens in combination with predators or parasitoids (Roy and Pell, 2000;
1552 Wraight, 2003. For example, Labbé et al. (2009) demonstrated that applications of *B. bassiana*
1553 for control of greenhouse whiteflies (*Trialeurodes vaporariorum*) was compatible with
1554 concurrent use of the parasitoid, *Encarsia formosa*, and the generalist predator, *Dicyphus*
1555 *hesperus*.

1556 Clearly, opportunities exist to use a variety of mechanisms to improve the efficiency of
1557 fungal biocontrol strategies. Such approaches can reduce the amount of inoculum needed to
1558 control a pest and provide protection against environmental factors that would otherwise rapidly
1559 degrade the organism post application, while improving efficacy and cost-effectiveness. This
1560 area needs to be explored further rather than remaining focused on the pesticide paradigm.

1561

1562 ***4.8 Conservation biological control***

1563 Contrary to the inoculative or augmentative approaches discussed above, conservation biocontrol
1564 relies on the modification of habitats or of crop management techniques to promote the impact of
1565 ecosystem service providers, specifically the natural activity of biocontrol agents within a crop
1566 system (Steinkraus, 2007; Pell et al., 2010). The successful use of this approach relies on a
1567 thorough understanding of the biology and ecology of the pest and the natural enemy complex
1568 and, in the case of fungi, conditions that promote the development of epizootics (Pell et al., 2010;
1569 Meyling and Hajek, 2010). Although conservation biocontrol may be considered to be in its
1570 infancy for entomopathogens, this tactic has been successfully used on a large scale. For
1571 example, predictive systems have been devised to inform farmers when conditions favor the
1572 development of natural epizootics of *Neozygites fresenii* in cotton aphids, reducing the need for
1573 other mitigation strategies (Steinkraus et al., 2002; Steinkraus, 2007). There are opportunities to
1574 create a new norm around the ‘use’ of these natural enemies. They do not necessarily create
1575 commercial opportunities for sale of bioinsecticides, however development of systems whereby
1576 environmental conditions can be manipulated to promote the natural incidence and efficacy of
1577 fungi can provide an environmentally friendly and efficacious method for pest management.
1578 Both entomophthoralean and hypocrealean entomopathogenic fungi can make a significant

1579 contribution to pest reduction and can form the foundation of an integrated crop management
1580 program (Meyling and Eilenberg, 2007; Pell, 2007; Pell et al., 2010).

1581 Greater adoption of fungal controls in agriculture will rely on achieving greater efficacy, cost
1582 reduction, and an ability to broaden the range of pest species that may be targeted. Many of these
1583 potential approaches go beyond the use of fungi as microbial pesticides, and require a more
1584 ecological approach to their application.

1585 There are several key areas where we must continue to derive new knowledge to advance the
1586 development and use of fungal controls. Detailed knowledge of fungal ecology is needed to
1587 better understand their role in nature and limitations in biological control. More efficient mass
1588 production, formulation, and delivery systems are needed to supply a larger market; most fungi
1589 are mass-produced using solid substrates and there are obvious physical limitations to the
1590 amount of inoculum that can be produced using these processes. More testing under field
1591 conditions is required to identify effects of biotic and abiotic factors and their interactions on
1592 efficacy, persistence, and potential limitations to the use of these biocontrol agents in certain
1593 crops or locations; and greater investment in the optimization of use practices is needed. There
1594 are great opportunities to use fungi in classical and conservation biological control approaches
1595 that can improve environmental stability, efficacy and the cost effectiveness.

1596 1597 **5. Entomopathogenic Nematodes**

1598 ***5.1 Background and overall status***

1599 Although there are numerous nematode taxa that have shown potential in biological control, the
1600 entomopathogenic nematodes (EPN), Rhabditida: Steinernematidae and Heterorhabditidae, have
1601 been most successful and have received the most attention (Grewal et al., 2005a), and therefore
1602 constitute the focus in this article. We include only a brief description of EPN basic biology and

1603 life cycles; more detailed aspects may be found elsewhere (e.g., Kaya and Gaugler, 1993;
1604 Gaugler, 2002; Grewal et al., 2005).

1605 EPNs kill arthropod hosts via a mutualistic symbiosis with bacteria, *Xenorhabdus* spp. and
1606 *Photorhabdus* spp. for steinernematids and heterorhabditids, respectively (Poinar, 1990).
1607 Infective juveniles (IJs), the only free-living stage, enter hosts through natural openings (mouth,
1608 anus, and spiracles), or in some cases, through the cuticle. After entering the host's hemocoel,
1609 nematodes release their bacterial symbionts, which are primarily responsible for killing the host
1610 within 24-48 hours, defending against secondary invaders, and providing the nematodes with
1611 nutrition (Dowds and Peters, 2002). The nematodes molt and complete up to three generations
1612 within the host, after which IJs exit the cadaver to find new hosts (Kaya and Gaugler, 1993).
1613 EPNs possess many positive attributes as biological control agents (Shapiro and Grewal, 2008).
1614 They are safe to humans and are generally safe to other nontarget organisms and the environment
1615 (Akhurst and Smith, 2002; Ehlers, 2005), which has led to a lack of pesticide registration
1616 requirements in many countries such as the United States and nations in the European Union
1617 (Ehlers, 2005). With few exceptions, e.g., *Steinernema scarabaei* (Koppenhöfer and Fuzy,
1618 2003), entomopathogenic nematodes have a wide host range. Some nematode species have been
1619 reported to infect dozens of insect species across five or more orders (Poinar, 1979; Klein, 1990),
1620 and certain nematode species are used commercially against 12 or more insect species (see Table
1621 4). Entomopathogenic nematodes are amenable to mass production using *in vivo* (infected
1622 insects) or *in vitro* (solid or liquid fermentation) methods (Shapiro-Ilan and Gaugler, 2002;
1623 Shapiro-Ilan et al., 2014a).

1624 A number of biotic and abiotic factors affect EPN pest control efficacy (Kaya and Gaugler,
1625 1993; Shapiro-Ilan et al., 2002a; Shapiro-Ilan et al., 2006a). Biotic factors such as choice of

1626 nematode species and rate of application (generally a minimum of 25 IJs per cm² is required) are
1627 critical (Shapiro-Ilan et al., 2002a). Environmental factors are also critical in determining
1628 efficacy of EPN applications (Shapiro-Ilan et al., 2006a; Shapiro-Ilan et al., 2012b). For
1629 example, the nematodes are highly sensitive to desiccation and ultraviolet light, thus applications
1630 made to soil or other cryptic habitats, and made during the early morning or evening, tend to be
1631 most successful. EPNs have been developed as biocontrol agents on a commercial level. They
1632 are currently being produced by at least 12 companies in Asia, Europe, and North America
1633 (Kaya et al., 2006), and, to date, at least 13 different species have reached commercial
1634 development, application, and sales: *Heterorhabditis bacteriophora*, *H. indica*, *H. marelata*, *H.*
1635 *megidis*, *H. zealandica*, *Steinernema carpocapsae*, *S. feltiae*, *S. glaseri*, *S. kushidai*, *S. kraussei*,
1636 *S. longicaudum*, *S. riobrave*, and *S. scapterisci* (Lacey et al., 2001; Georgis et al., 2006; Kaya et
1637 al., 2006; Shapiro-Ilan et al., 2014a). Commercial application extends to a considerable variety
1638 of economically important pests in various commodities (Table 4) (Shapiro-Ilan and Gaugler,
1639 2002; Georgis et al., 2006). Significant advances have increased the biocontrol utility of EPNs
1640 since 2001; new pests have been targeted, production and application technologies have been
1641 improved, and our fundamental knowledge of ecology and genetics has greatly expanded. The
1642 following is an update in research progress relative to EPN application since 2001.

1643

1644 **5.2 Novel EPN targets**

1645 The quest to develop EPNs for new target pests has remained active. High levels of efficacy have
1646 been demonstrated against previously untested (or insufficiently tested) insect pests. Most of the
1647 new targets are soil pests because the environment is favorable for EPNs. For example, EPNs
1648 have caused substantial field suppression (75 to 100%) in two root-boring pests of stone fruits,

1649 the Mediterranean flat-headed rootborer, *Capnodis tenebrionis* (L.) (Morton and Garcia-del-
1650 Pino, 2008; Martinez de Altube et al., 2008) and the peachtree borer, *Synanthedon exitiosa*
1651 (Cottrell and Shapiro-Ilan, 2006; Shapiro-Ilan et al., 2009a). In addition to root-borers, advances
1652 have been made in effectively controlling soil-dwelling stages of other insect pests, such as the
1653 filbertworm, *Cydia latiferreana* (Bruck and Walton, 2007; Chambers et al., 2010), guava weevil,
1654 *Conotrachelus psidii* (Dolinski et al., 2006), large pine weevil, *Hylobius abietis* L. (Dillon et al.,
1655 2007; Williams et al., 2013b), navel orangeworm, *Amyelois transitella* (Siegel et al., 2006),
1656 pecan weevil, *Curculio caryae* (Shapiro-Ilan et al., 2006b), plum curculio, *Conotrachelus*
1657 *nenuphar* (Shapiro-Ilan et al. 2004a, 2008a, 2013; Alston et al., 2005; Pereault et al., 2009),
1658 oriental fruit moth, *Grapholita molesta*, (Riga et al., 2006; De Carvalho et al., 2013), and small
1659 hive beetle, *Aethina tumida* (Ellis et al., 2010; Shapiro-Ilan et al., 2010a).

1660 New developments in EPN usage have also taken place in non-soil habitats. Because
1661 nematodes are sensitive to adverse environmental conditions, a major barrier to expanded use of
1662 EPNs has been difficulties encountered with application to aboveground targets. Nevertheless,
1663 some significant progress has been made in that arena over the past several years, including the
1664 application of *S. feltiae* for control of the sweetpotato whitefly, *Bemisia tabaci*, in the
1665 greenhouses (>80% control) (Cuthbertson, et al., 2007) and application of *S. carpocapsae* for
1666 control of *P. xylostella*, which is enhanced by a novel surfactant-polymer formulation (Schroer
1667 and Ehlers, 2005; Schroer et al., 2005). Furthermore, *S. carpocapsae* treatments for control of the
1668 lesser peachtree borer, *Synanthedon pictipes*, were greatly enhanced by a follow-up application
1669 of a sprayable gel that is commonly used for protecting structures from fire (Shapiro-Ilan et al.,
1670 2010b), and *S. carpocapsae* treatments resulted in high levels of suppression of the red palm
1671 weevil, *Rhynchophorus ferrugineus* when applied in a chitosan formulation (Llàcer et al., 2009).

1672 Applications of EPNs to apple tree trunks for control of codling moth, *C. pomonella*, were
1673 improved when the treatments included the sprayable fire-gel or wood flour foam as a protective
1674 agent (Lacey et al., 2010). Additionally, some promise has been demonstrated for using EPNs for
1675 control of stored product pests (Mbata and Shapiro-Ilan, 2005; Ramos-Rodriguez et al., 2006;
1676 Athanassiou et al., 2008).

1677 In addition to developing new targets for EPNs, significant expansion and improvements
1678 have been made in the control of a number of “traditional” target pests, i.e., those that have been
1679 considered commercial targets, or potential commercial targets, for over a decade. A case in
1680 point is the use of EPNs for control of white grubs (Coleoptera: Scarabaeidae). Advances in
1681 white grub control have been made based on the discovery of new highly virulent steinernematid
1682 and heterorhabditid species or strains, as well as an in-depth analysis of nematode-host
1683 specificity and elucidation of the mechanisms behind that specificity (e.g., differences in
1684 infection routes and optimum soil parameters) (Koppenhöfer and Fuzy, 2003; 2007; An and
1685 Grewal, 2007; Grewal et al., 2004; Koppenhöfer et al., 2006; 2007).

1686 A new discovery of particular promise is the recently discovered *S. scarabaei*, which is
1687 highly virulent against a variety of white grubs and exhibits long-term persistence in the soil
1688 environment (Stock and Koppenhöfer, 2003; Koppenhöfer and Fuzy, 2003; Koppenhöfer et al.,
1689 2009). Additionally, enhanced control of codling moth, *C. pomonella* was observed based on use
1690 of optimum application equipment, addition of adjuvants, and mulching (Unruh and Lacey,
1691 2001; Lacey et al., 2006a,b). A novel control approach for codling moth is to add EPNs to the
1692 water in apple dump tanks, thereby targeting the overwintering insects that are harbored in
1693 infested fruit bins (Lacey et al., 2005; de Waal et al., 2010). Advances in suppression have been
1694 made for other established target pests including fungus gnats (Diptera: Sciaridae) (optimized

1695 substrate media and timing of applications) (Cloyd and Zaborski, 2004; Jagdale et al., 2004;
1696 2007), the diaprepes root weevil, *Diaprepes abbreviatus* (expansion of control to other host
1697 plants) (Jenkins et al., 2008), grape root borer, *Vitacea polistiformis*, (Williams et al., 2010), and
1698 the western corn rootworm, *Diabrotica virgifera virgifera*, in Europe (Toepfer et al., 2008).

1699 Research has progressed significantly beyond direct application of EPNs as single control
1700 agents for suppression of insect pests. Studies on combining EPNs with other control tactics have
1701 increased substantially since 2001. Positive/synergistic interactions have been observed among
1702 various novel combinations with chemicals (Koppenhöfer et al., 2002; Polavarapu et al., 2007;
1703 Koppenhöfer and Fuzy, 2008; Reis-Menini et al., 2008), microbial agents (e.g., *M. anisopliae*
1704 *s.l.*) (Ansari et al., 2004; 2006a; Acevedo et al., 2007) and arthropod predators (Premachandra et
1705 al., 2003). However, neutral or negative interactions with these agents may also be observed
1706 depending on the specific pathogens, hosts, or application parameters (Koppenhöfer et al., 2002;
1707 Shapiro-Ilan et al.2004b). Interestingly, entomopathogenic nematodes have also been reported as
1708 synergists in conjunction with GM crops (i.e., Bt-corn) (Gassmann et al., 2008).

1709 EPN research has expanded beyond the targeting of insects pests to include such pests as
1710 plant-parasitic nematodes; efficacy in control of plant parasitic nematodes using EPNs has varied
1711 based on a number of factors such as target species and the cropping system (Lewis et al., 2001;
1712 Fallon et al., 2002; 2004; Jagdale et al., 2002, 2009; Nyczepir et al., 2004; Perez and Lewis
1713 2004; Lewis and Grewal, 2005; Shapiro-Ilan et al., 2006c). Finally, research has included
1714 utilization of nematode symbiotic bacteria partners (separate from the nematodes) or byproducts
1715 thereof, as control mechanisms for arthropods (Mohan et al., 2003; Jung and Kim, 2006;
1716 Bussaman et al., 2006; ffrench-Constant et al., 2007; Abdel-Razek, 2010; Da Silva et al., 2013)

1717 or plant pathogens (Isaacson and Webster, 2002; Ji et al., 2004; Böszörményi et al., 2009;
1718 Shapiro-Ilan et al., 2009b).

1719

1720 *5.3 Advances in basic research*

1721 Fundamental research on EPNs expands utility of the organisms in biological control efforts.
1722 Basic research in ecology of EPNs has progressed substantially in the past several years. For
1723 example, a number of advances in understanding the dynamics of host attraction and infection
1724 have been made. Novel cues eliciting EPN responses have been discovered including vibration
1725 (Torr et al., 2004), electromagnetic stimuli (Shapiro-Ilan et al., 2009c, 2012a; Ilan et al., 2013),
1726 and attraction to plant roots in response to chemical “distress calls” triggered by pest attack (van
1727 Tol et al., 2001; Rasmann et al., 2005; Ali et al., 2013). Plant roots were also found to enhance
1728 nematode infection by providing routes for nematode movement (Ennis et al., 2010). Infection
1729 and foraging behaviors such as jumping response (Campbell and Kaya, 1999; 2002), response to
1730 host exudates (Kunkel et al., 2006), differential response to infected vs. uninfected hosts
1731 (Christen et al., 2007; Ramos-Rodriguez et al., 2007), chemical signaling (Kaplan et al., 2012)
1732 and olfactory response (Dillman et al., 2012), and competition within the host (male fighting)
1733 (Zenner et al., 2014) have been elucidated. Additionally, broad models of host-parasite infection
1734 dynamics have been developed and/or tested, such as the phased infectivity hypothesis
1735 (Campbell et al., 1999; Dempsey and Griffin, 2002; Ryder and Griffin 2003), optimal infection
1736 strategies based on trade-offs (Fenton and Rands, 2004), risk-sensitive infection and “follow the
1737 leader” behavior (Fushing et al., 2009), and aggregative group movement/foraging behavior
1738 (Shapiro-Ilan et al., 2014b). These discoveries greatly expand our knowledge of factors that

1739 drive foraging and infection strategies (e.g., the discovery of aggregative movement suggests that
1740 nematodes may move together in the soil in groups, akin to a pack of wolves).

1741 Fundamental research has also progressed in the realm of soil ecology. Insight has been
1742 gained into interactions with other biotic agents such as phoretic associations (Campos-Herrera
1743 et al., 2006), an alternative role for EPNs as scavengers rather than parasites (San-Blas and
1744 Gowen, 2008), food web response and competition among entomopathogenic or non-
1745 entomopathogenic nematode species (Millar and Barbercheck, 2001; Somasekhar et al., 2002;
1746 Duncan et al., 2003a, 2003b, 2007; Hodson et al., 2012), and deterrence or susceptibility to
1747 antagonists (Zhou et al., 2002; El-Borai et al., 2009). Some of these relationships, e.g., phoretic
1748 associations causing enhanced EPN dispersal, have direct impacts toward improved biocontrol
1749 efficacy (Shapiro-Ilan and Brown, 2013). Additionally, advances were made in elucidating the
1750 impact of soil habitat complexity in reference to EPN spatial dynamics and trophic cascade
1751 theory (Efron et al., 2001; Spiridonov et al., 2007; Denno et al., 2008; Hoy et al., 2008; Jabbour
1752 and Barbercheck, 2008; Ram et al., 2008). Research focused on soil dynamics, such as the
1753 studies cited above, elucidate biotic and abiotic factors that impact nematode distribution and
1754 persistence and therefore directly impacts our ability to enhance efficacy of short-term
1755 inundative applications, and also serves as foundation for development of inoculative, classical,
1756 or conservation approaches (Loya and Hower, 2002; Preisser et al., 2005; Adjei et al., 2006;
1757 Barbara and Buss, 2006; Stuart et al., 2008).

1758 Expansion of basic research in entomopathogenic nematology has also been made through
1759 extensive progress in fundamental genetic studies including molecular genetics and genomics. Of
1760 particular note, the entire genomes of entomopathogenic nematodes and their symbionts have
1761 been sequenced (e.g., Duchaud et al., 2003; Bai and Grewal, 2007; Ciche, 2007; Bai et al., 2009,

1762 2013; Schwartz et al., 2011; Bai et al., 2013). Additional tools (i.e., RNAi) for evaluating
1763 functional genomics of the sequence as it becomes available have been developed (Ciche and
1764 Sternberg, 2007), and analyses of certain EPN genes and their expression have already been
1765 reported including genes related to stress, involvement in host colonization, and the host-
1766 pathogen relationship (Chen et al., 2006; Sandhu et al., 2006; Bai and Grewal, 2007; Tyson et
1767 al., 2007; Cowles and Goodrich-Blair, 2008; Hao et al., 2008; Somvanshi et al., 2008; Bai et al.,
1768 2009; Easom et al., 2010; Hao et al., 2012). Given the unique characters of EPN biology and the
1769 progress made in genetic studies, the entomopathogenic nematode-bacterium complex is being
1770 developed and recognized as model system for understanding pathogenicity and symbiosis
1771 (Goodrich-Blair, 2007; Clarke, 2008; Hussa and Goodrich-Blair, 2013).

1772 Although the outcomes may not be immediately apparent, advancements in molecular
1773 genetics and genomics will cultivate the development of new tools for enhancing biocontrol with
1774 EPNs. Additionally, significant progress has been made in applied genetic studies that may have
1775 more near-term benefits to EPN utility. For example, new EPN strains with enhanced traits (e.g.,
1776 environmental tolerance) have been developed through genetic improvement methods of
1777 selection and or hybridization (Strauch et al., 2004; Ehlers et al., 2005; Shapiro-Ilan et al., 2005;
1778 Nimkingrat et al., 2013). Beneficial trait deterioration is a significant problem that can occur
1779 during repeated EPN culturing; for example, virulence, environmental tolerance and reproductive
1780 capacity can decline after several passages *in vivo* (Bai et al., 2005; Bilgrami et al., 2006).
1781 Insights into the nature of beneficial trait deterioration (Bai et al., 2005; Bilgrami et al., 2006;
1782 Wang et al., 2007) as well as the discovery of methodologies to overcome the problem, e.g.,
1783 through the creation of homozygous inbred lines (Bai et al., 2005; Anbesse et al., 2013), and

1784 insight into the specific genes that change (Adhikari et al., 2009) will foster maintenance of
1785 strain stability and biocontrol performance.

1786

1787 ***5.4 Production and application technology***

1788 Considerable advances in EPN production and application technology have been made, including
1789 liquid culture media improvement (Gil et al., 2002; Islas-López et al., 2005; Chavarría-
1790 Hernández et al., 2006) and increased understanding of the EPN biology, population dynamics,
1791 and physical parameters within the bioreactor (Chavarría-Hernández and de la Torre, 2001; Han
1792 and Ehlers, 2001; Neves et al., 2001; Johnigk et al., 2004; Chavarría-Hernández et al., 2008;
1793 Hirao and Ehlers, 2010; Hirao et al., 2010; Belur et al., 2013). Detailed microbiological and
1794 molecular aspects of the EPN life-cycle have also been elucidated (Chaston et al., 2013;
1795 Moshavov et al., 2013). In vivo production of EPNs has been enhanced through the development
1796 of mechanized equipment (Gaugler et al., 2002) and improved inoculation procedures (Shapiro-
1797 Ilan et al., 2002b; Brown et al., 2006; Shapiro-Ilan et al., 2008b).

1798 Aqueous application has benefited from advanced understanding the impacts of various types
1799 of application equipment on the EPNs (Fife et al., 2003; 2004; 2006; Brusselman et al., 2012).
1800 Additionally, in terms of application technology, substantial interest in the approach of using
1801 infected host cadavers as a vehicle for EPN distribution has been garnered. In this approach,
1802 nematode infected hosts are applied to the target area and pest suppression is achieved by the
1803 progeny IJs that emerge from the insect cadavers. Over the past several years, a number of
1804 different pests have been targeted using the infected host application method (Bruck et al., 2005;
1805 Dillon et al. 2007; Del Valle et al., 2008; Jagdale and Grewal, 2008). Research has confirmed
1806 that, relative to application in aqueous suspension, infected host application can be superior in

1807 EPN infectivity, survival, dispersal, and pest control efficacy (Perez et al., 2003; Shapiro-Ilan et
1808 al., 2003b; Fujimoto et al., 2007). Moreover, studies indicate that the approach can be facilitated
1809 by formulating the infected hosts in coatings (Shapiro-Ilan et al., 2001; 2010a; Ansari et al.,
1810 2009; Del Valle et al., 2009) using hard-bodied insects as the host (Shapiro-Ilan et al., 2008c)
1811 and development of equipment to distribute the cadavers (Zhu et al., 2011). Nonetheless, the
1812 cadaver application method has thus far only been used commercially on a very small scale
1813 relative to conventional methods.

1814

1815 *5.6 The future for entomopathogenic nematodes*

1816 EPNs have been cultured commercially for more than 25 years. Substantial progress has been
1817 made in terms of the number of insect pests that are targeted as well as the number of different
1818 nematode species produced. Nonetheless, commercial level application has not reached
1819 expectations. In the 1980s and 1990s, companies projected sales of well over \$100 million, yet
1820 currently the market is closer to only 10% of those projections (Gaugler and Han, 2002; Georgis,
1821 2002). A number of barriers exist that have hindered further expansion of EPN markets including
1822 cost of product, efficacy, and shelf life. These barriers may be overcome through a variety of
1823 endeavors as outlined below.

1824 One approach to improving efficacy and expanding the list of target pests to which EPNs can
1825 be marketed is to improve the EPNs themselves. Methods to improve and expand the use of
1826 EPNs include discovery of more effective strains or species and genetic improvement via
1827 selection, hybridization or molecular manipulation (Gaugler, 1987; Burnell, 2002; Grewal et al.,
1828 2005b). Discovery of new strains and species is a straightforward approach that can quickly lead
1829 to enhanced efficacy based on innate differences in nematode virulence, environmental

1830 tolerance, or other properties. For example, in the 1990s, the discovery and subsequent
1831 commercialization of *S. scapterisci* for control of mole crickets and *S. riobrave* for *Diaprepes*
1832 root weevils and other insects made a considerable impact on EPN markets (Shapiro-Ilan et al.,
1833 2002a). The rate of EPN species discovery has been increasing dramatically (Poinar, 1990;
1834 Adams and Nguyen, 2002; Stock and Hunt, 2005). Of the more than 90 EPN species reported to-
1835 date (e.g., in the last nine decades) more than 40% have been described in the last decade (after
1836 2001). Additionally, the numerous new strains of existing species that are being discovered can
1837 also offer enhanced virulence or other properties (e.g., Stuart et al., 2004). Certainly the number
1838 of new strains and species will continue to rise, adding more potential options for biocontrol
1839 development. However, in order to leverage the advantages that strain/species discoveries offer,
1840 biocontrol characterization of these new organisms must keep pace with the survey/discovery
1841 research. Currently, less than 20% of the >35 species discovered since 2001 have been tested for
1842 biocontrol efficacy in the laboratory, greenhouse, or field; clearly there is significant untapped
1843 potential. In addition to expanded utility derived from discovery, we can also expect the
1844 upcoming advances in genomics (Bai and Grewal, 2007; Ciche, 2007; Bai et al., 2009, 2013) to
1845 offer substantial opportunities for directed strain improvement through genetic methods.

1846 Improved production, formulation and application technology will lead to improved
1847 efficacy. Production efficiency and reduced costs are expected with the recent significant
1848 increase in number of laboratories or companies that are researching liquid culture methodology
1849 as well as the renewed interest in developing efficient automated in vivo systems (de la Torre,
1850 2003; Ehlers and Shapiro-Ilan, 2005; Shapiro-Ilan et al., 2014a). Additionally, fruitful
1851 advancements are expected through implementation of novel approaches to application such as
1852 distribution of infected hosts, attract and kill methodologies, slow-release teabags, habitat

1853 manipulation, and prophylactic plant dips as well as advanced research on the impact of
1854 application equipment (Wright et al., 2005a; Hiltbold et al., 2012; Nielsen and Lewis, 2012;
1855 Duncan et al., 2013). In contrast to production technology, with a few exceptions, activity in
1856 development of improved formulation has lagged, and shelf life (particularly at room
1857 temperature) continues to be a barrier to expansion of EPN markets. Thus, creative solutions to
1858 developing superior formulations are needed; alternatively, new approaches to marketing e.g.,
1859 “fresh” marketing, where shelf life is not a substantial issue, may be an option.

1860 Commercial use will also expand as the list of target pests deemed suitable for application
1861 increases. As indicated above, research toward increasing the use of EPNs to control new or
1862 existing targets has been an active area of research over the past decade and we can expect that
1863 such efforts will continue. Expansion of target pests and markets depends largely on
1864 establishment of field efficacy. At a certain point, if innate virulence is too low then there is little
1865 chance for success (Shapiro-Ilan et al., 2002a). Thus, substantial research efforts have been
1866 devoted to determining field efficacy, and a large body of literature has demonstrated high levels
1867 (e.g., $\geq 75\%$) of control against numerous economically important pests (Klein, 1990; Shapiro-
1868 Ilan et al., 2002a; Grewal et al., 2005a) (Table 4). Note that some pests listed in Table 4 have
1869 never become significant commercial targets despite the fact that high levels of efficacy can be
1870 demonstrated under field conditions. Thus it is clear that efficacy is not the sole factor for
1871 establishing market success.

1872 It also should be noted that some of the commercial targets pests are not necessarily strongly
1873 supported by high levels of field efficacy (e.g., $\geq 75\%$) reported in several refereed papers.
1874 Possibly, some of these pests are not actually suitable for control with EPNs, but are listed as
1875 targets by some commercial companies nonetheless. In some of these cases however, it may be

1876 that substantial “in-house” research by EPN producers led to the existing markets. Alternatively,
1877 it may be that for some target pests, high levels of efficacy, similar to that expected for chemical
1878 pesticides, may not be necessary for EPN success.

1879

1880 **6. Commercialization**

1881 Although research into the use of entomopathogens as MCAs has been conducted for over 150
1882 years (Davidson, 2012) much of the effort has failed to lead to commercially successful
1883 microbial pesticide products. While some of the issues are related to biological constraints, a
1884 major factor is the absence of a clearly understood model for the commercialization of MCAs. A
1885 variety of factors contribute to the potential for market success, which is essentially a measure of
1886 cost and benefits including expected protection of the crop and crop value, and efficiency of
1887 competing products (Black et al., 1997; Shapiro-Ilan et al., 2002a; 2012b; Ravensberg, 2011;
1888 Glare et al., 2012). The development of MCAs is an extremely complex business, which many
1889 scientists fail to appreciate properly (Lisansky, 1997).

1890 The publication of the book *A Roadmap to the Successful Development and*
1891 *Commercialization of Microbial Pest Control Products* by Ravensberg (2011) is the first
1892 comprehensive attempt to analyze and communicate in a publically available single volume the
1893 entire process of developing products from entomopathogens. It is of particular value that
1894 examples were drawn from real product development projects and the author explains the
1895 regulatory and commercial challenges that may be unfamiliar to research scientists who are
1896 focused on biological studies, but that need to be addressed in developing research programs that
1897 will facilitate eventual commercialization.

1898 Registration is often identified as the biggest barrier to commercialization of MCAs
1899 (Montesinos, 2003; Chandler et al., 2008; Ravensberg, 2011; Sundh et al., 2012a). The issues

1900 around registration of MCAs have been discussed extensively in three recent books that
1901 addressed ways to simplify registration and reduce the costs for MCA development (Bailey et al.,
1902 2010; Ehlers, 2011; Sundh et al, 2012b). MCAs must be regarded as living entities within an
1903 ecosystem rather than simply as replacements for chemical pesticides (Sundh and Goettel, 2013).
1904 Kabuluk et al. (2010) compared in detail many registration systems used worldwide. The
1905 particular issues of developing successful MCA products for Africa have also been explored in
1906 some detail (Cherry and Gwynn, 2007; Grzywacz et al., 2009).

1907

1908 **7. Conclusions**

1909 Globally, pests annually consume the amount of food estimated to feed an additional one billion
1910 people (Birch et al., 2011). The human population is expected to grow from 6 billion today to 9
1911 billion in 2050 and the amount of food produced must increase commensurately. Increased crop
1912 production will mean increased amounts of food available for pests, with pest population
1913 increases and higher pest pressure as a consequence.

1914 The higher cost associated with the current generation of microbial pesticide products in
1915 comparison to most chemical insecticides is still considered a major limiting factor in many
1916 promising markets, especially in Asia and developing countries (Skovmand, 2007). The
1917 expanding global impact of Maximum Residue Limit regulations in removing older cheaper
1918 broad spectrum chemicals is expected to lower this barrier somewhat, although the ready
1919 availability of cheap “off patent” pesticides in many markets still constitutes a serious challenge
1920 to microbial pesticides.

1921 Glare et al. (2012) contend that MCAs have not yet reached their full potential, even though
1922 all predictions suggest microbial pesticides will outperform other pest control options in terms of
1923 market share increases in the near future. While the outlook for most microbial products is more

1924 positive than it has been for many years, there are a number of generic issues that will determine
1925 how much use expands in the near to long term future.

1926 Most MCAs are arthropod-specific, and most crops are likely to be affected by a suite of
1927 pests, therefore MCAs will need to be successfully integrated with other microbial products or
1928 pest management strategies in order to provide the pest control that farmers require. Several
1929 studies have been carried out to assess interactions of insect pathogens with chemical pesticides
1930 and fungicides. In general, few deleterious effects have been observed under field conditions and
1931 adverse effects observed in vitro were often not reliable predictors of antagonism under natural
1932 conditions. We cannot assume that all biocontrol agents, simply because they are living
1933 organisms, are compatible or interact positively, yet few studies have documented interactions
1934 among MCAs. The importance of such studies is evident, and clearly more research is needed to
1935 provide integrated, compatible, cost-effective and reliable bio-based pest control strategies for
1936 cropping systems, not only for individual crop pests. For example, synergistic virulence to the
1937 scarab, *Cyclocephala* spp., was observed for combinations of EPNs with *P. popilliae* (Thurston
1938 et al., 1993, 1994) or with *B. thuringiensis* subspecies *japonensis* (Koppenhöfer and Kaya, 1997;
1939 Koppenhöfer et al., 1999). However, interactions between entomopathogenic nematodes and
1940 other entomopathogens can also be antagonistic (Baur et al., 1998; Brinkman and Gardner, 2000;
1941 Koppenhöfer and Kaya, 1997; Shapiro-Ilan et al., 2004b). Advances in our understanding of
1942 infection processes, combined with the availability of new molecular tools that aid our ability to
1943 monitor the fate of entomopathogens in the environment and quantify effects of environmental
1944 factors on efficacy and persistence, continue to provide new insights that will support the rational
1945 development of these technologies.

1946 Legislation to increasingly restrict the residues of chemical pesticides in agricultural produce
1947 (including flowers and non-food products), is providing a major thrust for farmers to adopt non-
1948 chemical controls in place of chemical pesticides. Consumer awareness and demand is also
1949 driving major produce retailers to force growers to implement more sustainable pest and disease
1950 management techniques. This is creating new market opportunities for microbials and resulting
1951 in the expansion of the range of microbial products available to farmers. There seems little doubt
1952 that over the next decade major new opportunities to expand the use of microbials in agriculture
1953 will occur.

1954 However, while legislators are reducing the number of chemical pesticides and restricting
1955 their use, the regulatory agencies continue to operate in a regulatory framework for chemicals,
1956 which restricts progress by regulating microbial pesticides similarly to chemical insecticides.
1957 While there are moves to change regulations to create an easier pathway for the registration of
1958 biologicals, the current system remains a major impediment to the wider availability of microbial
1959 pesticides and their expanded use. Greater harmonization of registration practices across
1960 international boundaries, and acceptance of 'generic' safety data will help to streamline the
1961 registration process, and reduce the time and cost of bringing new microbial products to market.

1962 Microbial products, even when effective, must be able to compete successfully with other
1963 non-chemical technologies such as cultural controls, predators and parasitoids, on both cost and
1964 ease of use. This requires that research focuses on improving production techniques to lower
1965 costs and on formulation to improve storage and use, as well as on persistence to reduce the need
1966 for frequent application. A major task is to ensure that quality products are available and that
1967 farmers are equipped with the knowledge to apply them. By focusing resources on transitional

1968 research to devise robust practices, microbial pesticides can become important components of
1969 integrated crop production systems.

1970

1971 **8. Recommendations**

1972 Clear efforts must be made to engage stakeholders along the entire marketing chain including
1973 producers, regulators, farmers, retailers and consumers, to ensure acceptance and support of
1974 biocontrol approaches and the incorporation of MCAs in IPM strategies. Outreach and
1975 demonstration programs that promote understanding of what growers can (or cannot) expect
1976 from these control agents, coupled with appropriate training on their use, will further enhance
1977 their successful integration into agricultural production systems. Even though the climate for
1978 microbial pesticides is becoming more positive, significant research is still needed to overcome
1979 the limitations of current microbial products and expand the range of products available if they
1980 are to play a significantly greater role in the next generation of farming and pest control. Our
1981 recommendations to address these needs include:

- 1982 1. Continue the search for new entomopathogens. Given the withdrawal of chemical
1983 pesticides, new and diverse host-specific and multi-host entomopathogens are urgently
1984 needed. Pathogens can provide new efficacious MCAs and also the genetic diversity
1985 needed for adaptation to a wider range of habitats and climates. New entomopathogens
1986 can also serve as sources of novel genes for insect resistance and other advantageous
1987 traits that can be incorporated into the genomes of other microorganisms or plants.
- 1988 2. Continue development of production, formulations and application methods that will
1989 improve the efficacy, user acceptability and cost efficiency of MCAs for a variety of
1990 crops and climates.

- 1991 3. Focus on strategic selections of target pests and markets to meet the challenge of
1992 developing non-chemical control of global pests, including disease vectors. Control of
1993 vectors of human, animal and plant diseases is a growing global public priority and MCA
1994 research needs to address these targets.
- 1995 4. Continue development of transgenic plants using MCA genes for additional major crops.
1996 Develop objective and evidence-based knowledge to increase public understanding of
1997 transgenic crops.
- 1998 5. Adopt streamlined registration procedures for MCAs and harmonize global registration
1999 systems.
- 2000 6. Conduct further studies on the ecology of insect pathogens and their role in the
2001 environment, which will increase their potential for efficient and sustainable use in pest
2002 management.

2003

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2013

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4459 *farinosus*) and the *Isaria fumosorosea* species complex (formerly known as *Paecilomyces*
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4461 *Technology* 18, 865-901.
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4463 Table 1. Entomopathogenic viruses that have been used for biological control of insect pests.
4464

| Common and Species Names | Targeted insects | Producer | Selected References |
|---------------------------------------------------|------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------|
| Baculovirus | Principally Lepidoptera, some Hymenoptera and Diptera | | Miller (1997), Moscardi (1999, 2007), Theilmann et al. (2005), Szewczyk et al. (2009), Harrisson and Hoover (2012) |
| Corn earworm NPV (HezeSNPV) | <i>Helicoverpa zea</i> : Corn earworm, Tomato fruitworm, Tobacco budworm. <i>Heliothis virescens</i> | Certis (USA) | Ignoffo (1999), Rowley et al. (2011) |
| Cotton bollworm NPV (HearNPV) | <i>Helicoverpa armigera</i> , Cotton bollworm, Podborer, | Andermatt, (Switzerland) AgBioTech (Australia) Jiyuan Baiyun Industry Company Ltd (China), BioControl Research Labs (India), Kenya Biologics (Kenya), plus other producers in India, China, | Grzywacz (2010), Hauxwell et al. (2010), Rabindra and Rowley et al. (2011), Yang et al., (2012), Gwynn (2014). |
| Diamond back moth GV (PlxyGV) | <i>Plutella xylostella</i> | Jiyuan Baiyun Industry Company Ltd (China) | Grzywacz et al. (2004), Farrar et al. (2007), Yang et al. (2012) |
| Unbarred Spodoptera moth (army worm NPV (SdalNPV) | <i>Spodoptera albula (sunia)</i> | Agricola el Sol (Guatamala) | Moscardi (1999) |
| Beet armyworm NPV (SpexMNPV) | <i>Spodoptera exigua</i> | Andermatt, (Switzerland) Certis (USA) Jiyuan Baiyun Industry Company Ltd, (China) BioTech (Thailand) | Kolodny-Hirsch et al. (1997), Lasa et al. (2007), Sun and Peng (2007), Gwynn (2014) |
| Egyptian Cotton Leafworm NPV | <i>Spodoptera littoralis</i> | Andermatt (Switzerland) | Jones et al. (1994) |

| | | | |
|---------------------------------------------------|------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------|
| (SpliNPV) | | | |
| Tobacco armyworm NPV (SpltNPV) | <i>Spodoptera litura</i> | Biocontrol Research Lab, Ajay Biotech, Bassarass Biocontrol, Biotech International, BioControl Research Labs (India) Jiyuan Baiyun Industry Company Ltd, (China) | Nakai and Cuc (2005), Department of Biotechnology India (2007), Kunimi (2007), Yang et al. (2012) |
| Gypsy moth, NPV (LydiMNPV) | <i>Lymantria dispar</i> | USDA , (USA) Sylvar Technology (Canada) Andermatt (Switzerland) | Podgewaite (1999) |
| Velvetbean caterpillar, NPV (AngeMNPV) | <i>Anticarsia gemmatalis</i> | Coodetec. CNP So, Nova Era Biotecnologica Agricola, Nital Urbana Laboratorios, Coop Central Milenio Agro Ciencias (Brazil) | Moscardi (2007), Sosa-Gómez et al. (2008), Moscardi et al. (2011), Panazzi (2013) |
| Red headed pine sawfly NPV (NeleNPV) ¹ | <i>Neodiprion lecontei</i> | Sylvar Technology (Canada) | Cunningham (1995) |
| Douglas fir tussock moth NPV (OrpsNPV) | <i>Orygia pseudotsugata</i> | Canadian Forest Service | Martignoni (1999) |
| Balsam fir sawfly NPV (NeabNPV) | <i>Neodiprion abietis</i> | Sylvar Technology (Canada) | Lucarotti et al. (2007), Moreau and Lucarotti (2007) |
| Codling moth GV (CpGV) | <i>Cydia pomonella</i> | Certis (USA), BioTepp (Canada), Arysta Lifscience(France), Andermatt (Switzerland), Hoerst (Germany), BioBest (Belgium), Arysta Life Science (France), Agro Roca (Argentina) | Tanada (1964), Cross et al. (1999), Arthurs et al. (2005); Eberle and Jehle (2006), Lacey et al. (2008b) |
| False Codling Moth GV | <i>Cryptophlebia</i> | Andermatt | Singh et al. (2003), |

| | | | |
|-------------------------------------------|---------------------------------------------|------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------|
| (CrleGV) | <i>leucotreta</i> | (Switzerland), River Bioscience (South Africa) | Moore et al. (2004b) |
| Potato tuber moth GV (PhopGV) | <i>Phthorimaea operculella</i> | Centro Internacional de la Papa (Peru), Proinpa (Bolivia) | Sporleder (2003), Arthurs et al. (2008b), Kroschel and Lacey (2008), Lacey and Kroschel (2009) |
| Summer fruit tortrix GV (AdorGV) | <i>Adoxophyes orana</i> | Andermatt (Switzerland) | Blommers (1994), Cross et al. (2005), Nakai (2009) |
| Tea tortrix (HomaGV) | <i>Homona magnanima</i> | Arysta life science (Japan) | Kunimi (2007), Nakai (2009) |
| Smaller Tea tortrix GV (AdhoGV) | <i>Adoxophyes honmai</i> | Arysta life science (Japan) | Nakai et al. (2002), Nakai (2009) |
| Alfalfa looper NPV (AucaMNPV) | Noctuidae | Agricola el Sol (Guatamala) | Vail et al. (1999), Yang et al. (2012) |
| Cabbage looper (TrniSNPV) [†] | <i>Trichoplusia ni</i> | Andermatt (Switzerland) | Vail et al. (1999) |
| Tea geometrid EcobNPV | <i>Extropia obliqua</i> | Small scale commercial production China * | Sun and Peng (2007), Yang et al. (2012) |
| Tea tussock moth (Eups NPV) | <i>Euproctis pseudoconsersa</i> | Small scale commercial production China * | Sun and Peng (2007), Yang et al. (2012) |
| Tea Moth (BuzuNPV) | <i>Buzura suppressaria</i> | Small scale commercial production China * | Sun and Peng (2007), Yang et al. (2012) |
| Teak Defoliator (HypeNPV) | <i>Hylea peura</i> | Kerala Forest Research Institute (India) | Nair et al. (1996) |
| Imported cabbageworm (PiraGV) | <i>Artogeia (Pieris) rapae</i> | Registered in China Small scale commercial production China * | Yang et al. (2012) |
| Oriental armyworm, (LeseNPV) | <i>Leucania (Mythimna) separata</i> | Registered in China Small scale commercial | Yang et al. (2012) |

| | | | |
|----------------------------------|-------------------------------|----------------------------------------------------------------------|--------------------------------------------------------------------------|
| | | production China * | |
| Reoviridae | | | |
| Masson pine moth cypovirus (CPV) | <i>Dendrolimus punctatus</i> | Registered in China Small scale commercial production China * | Peng et al. (2000), Yang (2007) Yang et al. (2012) |
| Parvoviridae | | | |
| Cockroach densovirus (DNV) | <i>Periplaneta fuliginosa</i> | Registered in China Small scale commercial production China * | Bergoin and Thijsen (1997), Yang et al. (2012) |
| Nudiviruses | | | |
| Oryctes virus | <i>Oryctes rhinoceros</i> | Not commercially produced but locally produced for autodissemination | Jackson et al. (2005), Huger (2005), Ramle et al. (2005), Jackson (2009) |

4465 * Personal Communications. Professor Xiulian Sun Wuhan Institute Virology

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4467 Table 2. Entomopathogenic bacteria used for control of insect pests of major crops, forest, turf,
 4468 humans and domesticated animals.
 4469

| Bacterial Species | Major Targeted Habitat | Examples of Major Pest Orders | Selected References |
|------------------------------------------------------------------------|-------------------------------------------|---------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------|
| <i>Bacillus thuringiensis</i> sub-species <i>kurstaki</i> ¹ | Row crops, forests, orchards | Lepidoptera: numerous families and species | Glare and O'Callaghan (2000), Federici (2005), Huang et al. (2007), Lacey et al. (2007), van Frankenhuyzen (2009), Jurat-Fuentes and Jackson (2012), |
| <i>B. thuringiensis</i> sub-species <i>aizawai</i> ¹ | Row crops, orchards | Lepidoptera | Tabashnik et al. (1993), Glare and O'Callaghan (2000), Mashtoly et al. (2011) |
| <i>B. thuringiensis</i> sub-species <i>tenebrionis</i> ¹ | Potato | Coleoptera: Chrysomelidae, predominantly <i>Leptinotarsa decemlineata</i> | Kreig et al. (1983), Langenbruch (1985), Gelernter (2002) |
| <i>B. thuringiensis</i> sub-species <i>israelensis</i> ¹ | Diverse lentic and lotic aquatic habitats | Diptera: Culicidae and Simuliidae | Lacey and Merritt (2003), Lacey (2007), Skovmand et al. (2007), Despres et al. (2011) |
| <i>B. thuringiensis</i> sub-species <i>japonensis</i> strain Buibui | Lawn and turf | Coleoptera: Scarabaeidae | Alm et al. (1997), Klein et al. (2007), Mashtoly et al. (2010) |
| <i>Lysinibacillus sphaericus</i> ¹ | Lentic aquatic habitats | Diptera: Culicidae | Charles et al. (2000), Lacey (2007), Skovmand et al. (2007) |
| <i>Paenibacillus popilliae</i> | Lawn and turf | Coleoptera: Scarabaeidae: <i>Popillia japonica</i> | Klein et al. (2007), Koppenhöfer et al. (2012) |
| <i>Serratia entomophila</i> ¹ | Pasture | Coleoptera: Scarabaeidae: <i>Costelytra zealandica</i> | Jackson et al. (1992, 2001), Jackson (2003), Jackson and Klein (2006) |

4470 ¹commercially produced

4471

4472 Table 3. An overview of the entomopathogenic fungi that have been developed for microbial
 4473 control of insect pests.¹

4474

| Species Names | Targeted insects | Produced in | Selected References |
|------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------|
| <i>Aschersonia aleyrodica</i> | Hemiptera (Aleyrodidae) | Russia | Fransen, 1990; Meekers et al., 2002; Lacey et al., 2008; McCoy et al., 2009 |
| <i>Beauveria bassiana sensu lato</i> | Acari, Coleoptera, Diplopoda, Diptera, Hemiptera, Hymenoptera, Isoptera, Lepidoptera, Orthoptera, Siphonoptera, Thysanoptera, | Africa, Asia, Australia, Europe, South & North America | de la Rosa et al., 2000; Wraight et al., 2000, 2007b; Chandler et al., 2005; Wekesa et al., 2005; Brownbridge et al., 2006; Labbé et al., 2009 |
| <i>Beauveria brongniartii</i> | Coleoptera (Scarabaeidae) | Europe, Colombia, Reunion Island | Zimmermann, 1992; Keller, 200; Keller et al., 2003; Dolci et al., 2006; Townsend et al., 2010 |
| <i>Conidiobolus thromboides</i> | Acari Hemiptera, Thysanoptera | Colombia, India, South Africa | Papierok and Hajek, 1997; Nielsen and Hajek, 2005; Hajek et al., 2012 |
| <i>Hirsutella thompsonii</i> | Acari | India | McCoy, 1981; Chandler et al., 2000, 2005; McCoy et al., 2009 |
| <i>Isaria fumosorosea</i> | Acari, Diptera, Coleoptera, Hemiptera, Thysanoptera, | Belgium, Colombia, Mexico, USA, Venezuela | Wraight et al., 2000, 2007; Lacey et al., 2008, 2011; Zimmermann, 2008 |
| <i>Lagenidium giganteum</i> | Diptera (Culicidae) | USA | Kerwin and Petersen, 1997; Skovmand et al., 2007 |
| <i>Lecanicillium longisporum</i> | Hemiptera | Brazil, Netherlands | Bird et al., 2004; Down et al., 2009; Kim et al., 2009 |
| <i>Lecanicillium muscarium</i> | Acari, Hemiptera, Thysanoptera | Netherlands, Russia | Chandler et al., 2005; Cuthbertson and Walters, 2005; Burges, 2007; Goettel et al., 2008 |
| <i>Metarhizium anisopliae sensu lato</i> | Acari, Blattoidea, Coleoptera, Diptera, Hemiptera, Isoptera, Lepidoptera, Orthoptera, | Africa, Asia, Australia, Europe, South, Central & North America | de la Rosa et al., 2000; Chandler et al., 2005; Wekesa et al., 2005; Jaronski and Jackson, 2012; Lacey et al., 2011 |

| | | | |
|----------------------------|-------------|------------------------------|----------------------------------------------------|
| <i>Metarhizium acridum</i> | Orthoptera | Australia, South Africa, USA | Lomer et al, 1999. 2001; Thomas, 2000 |
| <i>Nomuraea rileyi</i> | Lepidoptera | Columbia, India | Moscardi and Sosa-Gomez, 2007; Thakre et al., 2011 |
| | | | |

4475 ¹ Condensed and modified from de Faria and Wraight, 2007. For up to date information on
4476 products registered in the OECD Countries, visit [https://www5.agr.gc.ca/MPDD-CPM/search-](https://www5.agr.gc.ca/MPDD-CPM/search-recherche.do?lang=eng)
4477 [recherche.do?lang=eng](https://www5.agr.gc.ca/MPDD-CPM/search-recherche.do?lang=eng)
4478 For information on the production and successful use of entomopathogenic fungi as microbial
4479 pesticides in Latin America see Alves et al., 2008.

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 4484 Table 4. Efficacy and commercialization of entomopathogenic nematodes for suppression of
 4485 some major insect pests.

| Pest | Pest | Key | ≥ 75% Efficacy | Targeted |
|-----------------------|------------------------------------------------------|---------------------------|--------------------------------|---------------------------------|
| Common name | Scientific name | Crop(s) targeted | Observed^a | Commercially^c |
| Artichoke plume moth | <i>Platyptilia carduidactyla</i> | Artichoke | Yes (Sc) | Yes |
| Armyworms | Lepidoptera: Noctuidae ^b | Vegetables | Yes (Sc, Sf, Sr) | Yes |
| Banana moth | <i>Opogona sachari</i> | Ornamentals | Yes (Hb, Sc) | Yes |
| Banana root borer | <i>Cosmopolites sordidus</i> | Banana | Yes (Sc, Sf, Sg) | Yes |
| Billbug | <i>Sphenophorus</i> spp. (Coleoptera: Curculionidae) | Turf | Yes (Hb,Sc) | Yes |
| Black cutworm | <i>Agrotis ipsilon</i> | Turf, vegetables | Yes (Sc) | Yes |
| Black vine weevil | <i>Otiorhynchus sulcatus</i> | Berries, ornamentals | Yes (Hb, Hd, Hm, Hmeg, Sc, Sg) | Yes |
| Borers | <i>Synanthedon</i> spp. and other sesiids | Fruit trees & ornamentals | Yes (Hb, Sc, Sf) | Yes |
| Cat flea | <i>Ctenocephalides felis</i> | Home yard, turf | No | Yes |
| Chinch bugs | Hemiptera: Blissidae | Turf | No | Yes |
| Citrus root weevil | <i>Pachnaeus</i> spp. (Coleoptera: Curculionidae) | Citrus, ornamentals | Yes (Sr, Hb) | Yes |
| Codling moth | <i>Cydia pomonella</i> | Pome fruit | Yes (Sc, Sf) | Yes |
| Corn earworm | <i>Helicoverpa zea</i> | Vegetables | Yes (Sc, Sf, Sr) | Yes |
| Corn rootworm | <i>Diabrotica</i> spp. | Vegetables | Yes (Hb, Sc) | Yes |
| Cranberry girdler | Chrysoteuchia topiaria | Cranberries | Yes (Sc) | Yes |
| Crane fly | Diptera: Tipulidae | Turf | Yes (Sc) | Yes |
| Diamondback moth | Plutella xylostella | Vegetables | No | Yes |
| Diaprepes root weevil | Diaprepes abbreviatus | Citrus, ornamentals | Yes (Hb, Sr) | Yes |
| Fungus gnats | Diptera: Sciaridae | Mushrooms, greenhouse | Yes (Sf, Hb) | Yes |
| German cockroach | <i>Blattella germanica</i> | Household | No | Yes |
| Grape root borer | <i>Vitacea polistiformis</i> | Grapes | Yes (Hz) | No |
| Iris borer | <i>Macronoctua onusta</i> | Iris | Yes (Hb, Sc) | Yes |
| Large pine weevil | <i>Hylobius abietis</i> | Forest plantings | Yes (Hd, Sc) | Yes |

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|------------------------|----------------------------------------------|-------------------------|---------------------------------------|-----|
| Leafminers | <i>Liriomyza</i> spp. (Diptera: Agromyzidae) | Vegetables, ornamentals | Yes (Sc, Sf) | Yes |
| Mint flea beetle | <i>Longitarsus waterhousei</i> | Mint | No | Yes |
| Mint root borer | <i>Fumibotys fumalis</i> | Mint | No | Yes |
| Mole crickets | <i>Scapteriscus</i> spp. | Turf | Yes (Sc, Sr, Scap) | Yes |
| Navel orangeworm | <i>Amyelois transitella</i> | Nut and fruit trees | Yes (Sc) | Yes |
| Oriental fruit moth | <i>Grapholita molesta</i> | Fruit trees | Yes (Sf) | No |
| Pecan weevil | <i>Curculio caryae</i> | Pecan | Yes (Sc) | Yes |
| Plum curculio | <i>Conotrachelus nenuphar</i> | Fruit trees | Yes (Sr) | Yes |
| Scarab grubs | Coleoptera: Scarabaeidae | Turf, ornamentals | Yes (Hb, Sc, Sg, Ss, Hz) ^b | Yes |
| Shore flies | <i>Scatella</i> spp. | Ornamentals | Yes (Sc, Sf) | Yes |
| Sod webworms | Lepidoptera: Pyralidae | Turf | No | Yes |
| Strawberry root weevil | <i>Otiorhynchus ovatus</i> | Berries | Yes (Hm) | Yes |
| Sugarbeet weevil | <i>Temnorhinus mendicis</i> | Sugar beets | Yes (Hb, Sc) | No |
| Sweetpotato weevil | <i>Cylas formicarius</i> | Sweet potato | Yes (Hb, Sc, Sf) | Yes |
| Wireworms | Coleoptera: Elateridae | Vegetables | No | Yes |

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4489 ^a At least one scientific paper reported $\geq 75\%$ suppression of these pests in the field or greenhouse.4490 Hb=*Heterorhabditis bacteriophora*, Hd = *H. downesi*, Hm= *H. marelatus*, Hmeg = *H. megidis*, Hz = *H.*4491 *zealandica*, Sc=*Steinernema carpocapsae*, Sf=*S. feltiae*, Sg=*S. glaseri*, Sk = *S. kushidai*, Sr=*S. riobrave*,4492 Sscap=*S. scapterisci*, Ss = *S. scarabaei*.

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4494 ^b Efficacy against various pest species within this group varies among nematode species.

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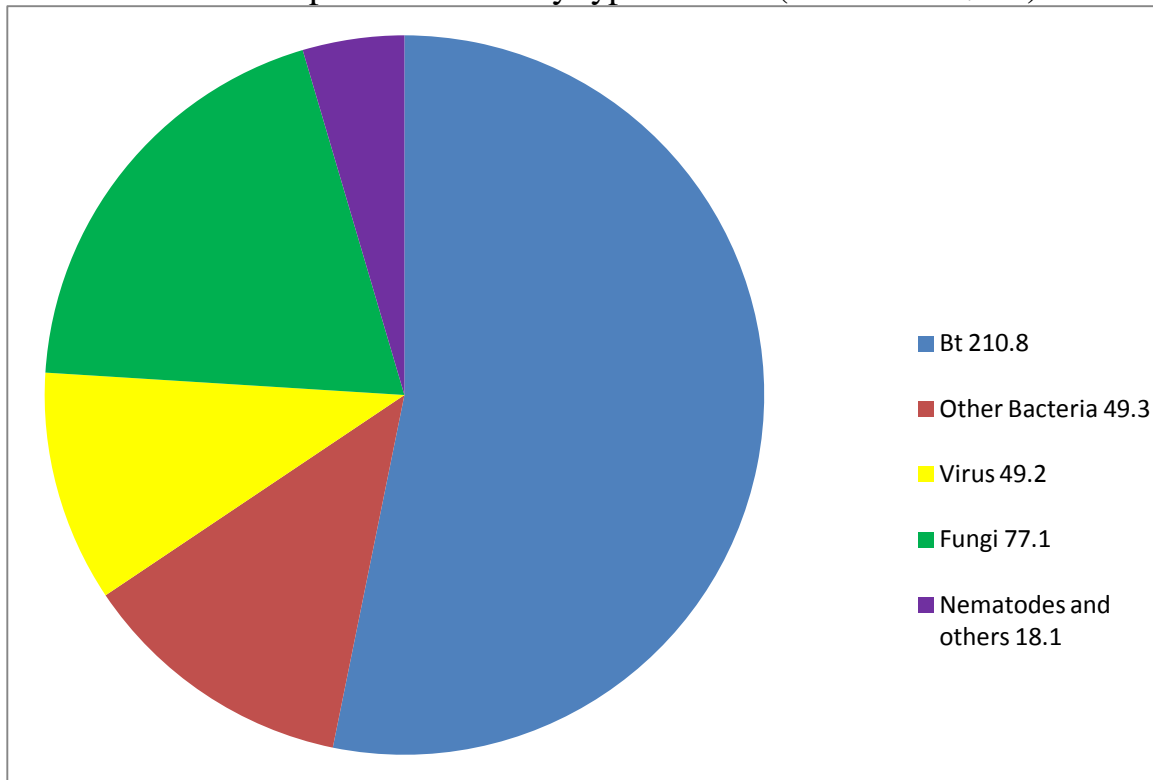
4496 ^c <http://www.biocontrol.entomology.cornell.edu/pathogens/nematodes.php>

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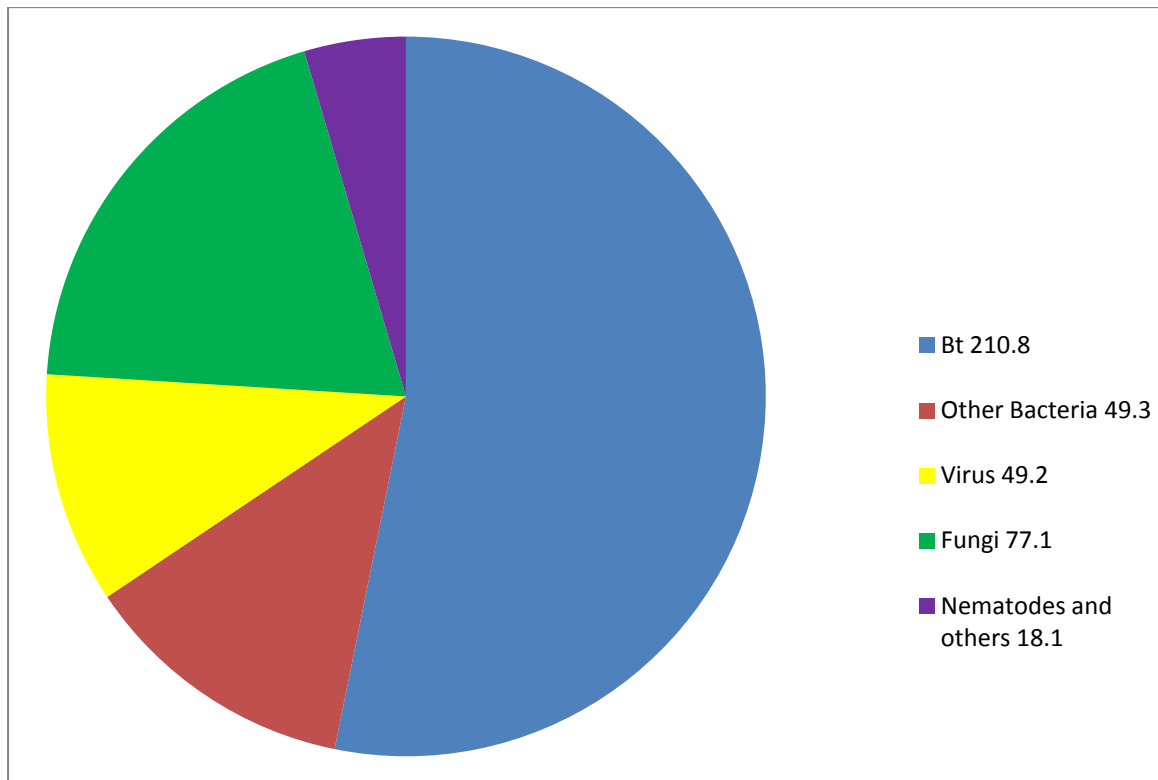
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4500 Estimated world biopesticide sales by type in 2010 (millions of \$US).



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4502 CPL Business Consultants (2010) The 2010 Worldwide Biopesticides Market Summary, (Vol.
4503 1), CAB International Centre. Wallingford.
4504

Figure 1. Estimated world biopesticide sales by type in 2010 (millions of \$US).



CPL Business Consultants (2010) The 2010 Worldwide Biopesticides Market Summary, (Vol. 1), CAB International Centre. Wallingford.

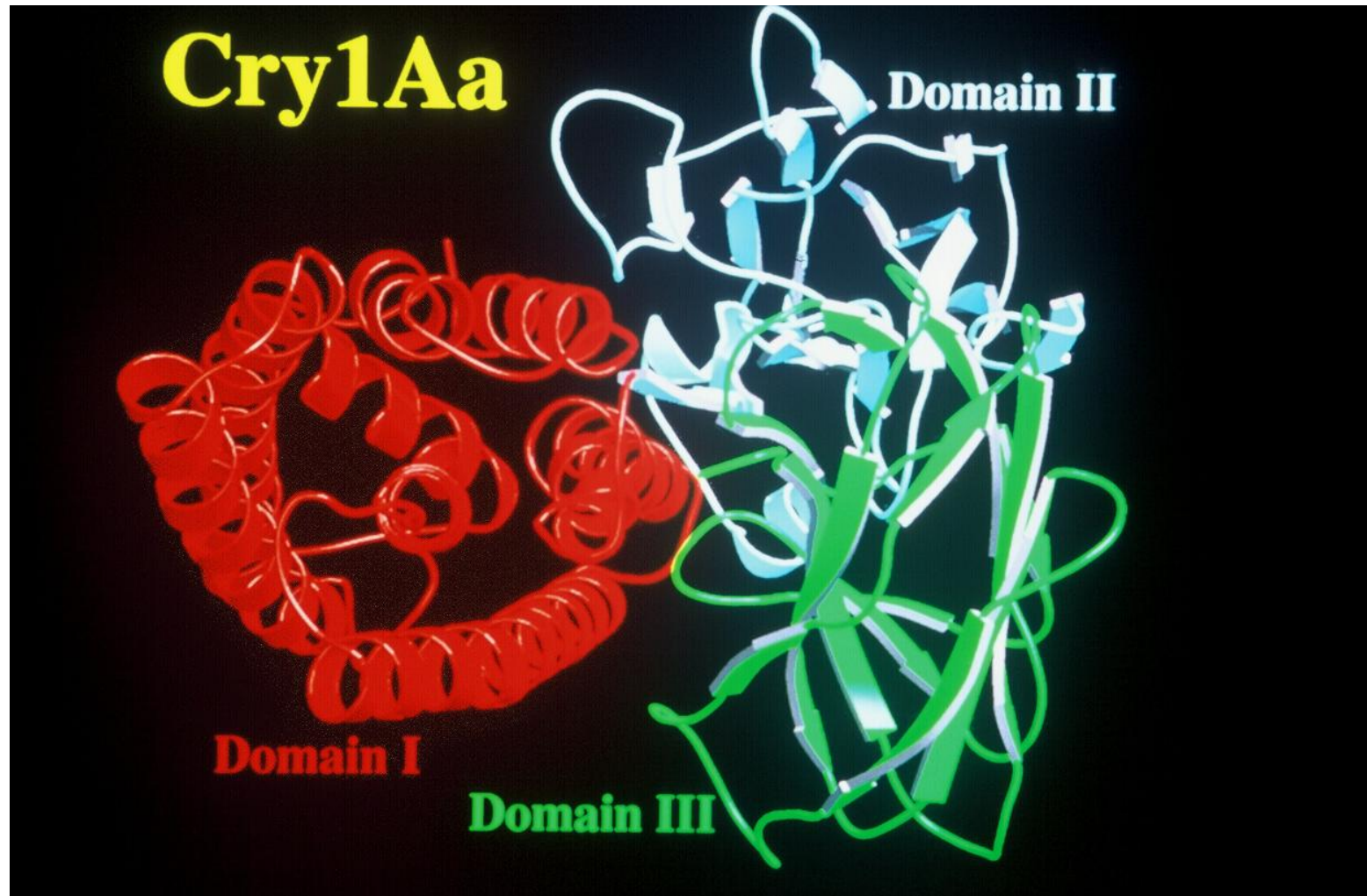


Figure 2. Apical ribbon view representing the 3-D structure of the *Bacillus thuringiensis* Cry1Aa toxin.