



2 Recent trends in management strategies for two major maize borers: 3 *Ostrinia nubilalis* and *Sesamia nonagrioides*

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7 Received: 13 May 2022 / Revised: 2 November 2022 / Accepted: 3 February 2023
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9 Abstract

10 Stem borers (Lepidoptera) are common cereal pests. In many parts of the world, the species *Ostrinia nubilalis* and *Sesamia*
11 *nonagrioides* stand out as important insect pests of economically important crops such as maize. Their management relied
12 mainly on transgenic host plant resistance over the last 25 years. Technologies based on the insecticidal properties of *Bacil-*
13 *lus thuringiensis*-derived proteins allowed widespread pest population suppression, especially for *O. nubilalis*. However, the
14 recent discovery of *Bt* resistance, which has revitalized interest in both pests' biology and management, may jeopardize the
15 effectiveness of such transgenic technologies. Historical information on *O. nubilalis* bionomy may need to be reassessed in
16 light of changing climate conditions and changing agricultural practices, as well as increased production of alternate host
17 crops across its distribution range. The current paper examines the bioecology and historical research that has been conducted
18 to manage these two important maize-boring pests.

19 **Keywords** Maize agroecosystems · Stem borers · Bioecology · Integrated Pest Management · Biological control

20 Introduction

21 Many agricultural crops are affected by stem borers from
the Crambidae and Noctuidae families (Albajes et al. 2002; 22
Agusti et al. 2005; Folcher et al. 2009). Stem borers' larvae 23

A1 Communicated by Antonio Biondi.

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24 feed by tunneling on the vegetative tissues of host plants,
 25 resulting in direct qualitative and quantitative yield losses.
 26 The European corn borer, *Ostrinia nubilalis* Hübner (Lepi-
 27 doptera: Crambidae), is a cosmopolitan species attacking
 28 a wide range of robust herbaceous plants (Capinera 2000).
 29 The Mediterranean corn borer *Sesamia nonagrioides* Lefeb-
 30 vre (Lepidoptera: Noctuidae) is a polyphagous species with
 31 a broad host range, primarily feeding on plants within the
 32 Poaceae family (Cruz and Eizaguirre 2016; Camargo et al.
 33 2020). However, both economically important pest species
 34 have a strong preference for maize (*Zea mays* L.) as a host
 35 plant in their areas of distribution (Pedigo and Rice 2009;
 36 Cruz and Eizaguirre 2016). *Sesamia nonagrioides* and *O.*
 37 *nubilalis* are the main pests of maize crops in those Mediter-
 38 ranean countries where considerable damage by larvae has
 39 been reported (Malvar et al. 2002). Furthermore, contami-
 40 nation from fungal pathogens entering through larval entry
 41 holes in the maize stalk or ear can degrade grain quality.

42 Integrated Pest Management (IPM) is a control strategy
 43 relying on the monitoring of insect populations and the use
 44 of environmental resources to control potential pests in an
 45 economic, ecological, toxicological, social, and long-term
 46 satisfactory manner. In contrast to the traditional pest control
 47 strategy, IPM denotes an approach in which a combination
 48 of methods is used to manage pest populations while taking
 49 into account environmental impacts and economic efficiency.
 50 IPM integration in modern agriculture has resulted in recent
 51 technological advances in pest management and increased
 52 public awareness of food safety and a healthy-living environ-
 53 ment. In countries where the *Bt* technology is not allowed
 54 like most of the European countries, stem borers' conven-
 55 tional control relies on the foliar spray of broad-spectrum
 56 synthetic insecticides, with well-known side effects includ-
 57 ing negative impacts on nontarget organisms and the risk
 58 of resistance development. Besides chemical control, one
 59 of the most used control tactics against stem borers is the
 60 cultivation of transgenic maize events expressing *Bt* pro-
 61 teins. The development of resistance in targeted lepidopteran
 62 pests is a potential concern for the widely used and very
 63 effective *Bt* technology. Only very few reports pointed out
 64 that *Bt* transgenic maize expressing Cry1F that had been
 65 successfully controlling *O. nubilalis* populations in the past
 66 is no longer attaining high levels of pest mortality in some
 67 regions of North American countries like Canada, while *O.*
 68 *nubilalis* populations from Europe remain susceptible to
 69 Cry1Ab-expressing maize (Thieme et al. 2018; Smith et al.
 70 2019). The development of *O. nubilalis* resistant populations
 71 may be variable in different geographic locations depend-
 72 ing on the environmental conditions, *Bt* proteins that are
 73 employed in a regional scale in maize or other crops, level
 74 of adoption of structured refuge areas, and the possibility
 75 of cross-resistance. Therefore, the deployment of efficient
 76 multi-tactics IPM strategies is warranted to keep stem borer

77 populations below economic injury levels as these pests can
 78 become more problematic in damaging transgenic maize in
 79 the following years.

80 As stem borers continue to be problematic in maize fields
 81 worldwide, knowledge about these economically important
 82 pest species and research on control methods need to be
 83 updated. To effectively manage stem borers, several control
 84 methods must be integrated into multi-tactic pest manage-
 85 ment programs. Commercial pheromone-based products
 86 for monitoring, decision-making support tools, and mating
 87 disruption should be used in conjunction with biological
 88 control using natural enemies such as predators, parasitoids,
 89 as well as entomopathogens. Novel approaches associating
 90 conventional breeding for resistance to corn stemborers with
 91 RNAi breakthroughs must be adopted to find applications in
 92 managing populations of lepidopteran pests. Chemical-based
 93 methods will continue to be one of the most popular control
 94 tactics for managing lepidopteran pests even though they can
 95 be challenging to apply for stem borer control, especially
 96 in areas where farmers have not yet adopted *Bt* maize pro-
 97 duction. Therefore, we present a comprehensive review of
 98 recent trends in IPM options and programs used in regions
 99 where the two major maize borer pests, *O. nubilalis* and *S.*
 100 *nonagrioides*, are found.

101 **Geographic distribution and bioecology** 102 **of maize stem borers *Ostrinia nubilalis*** 103 **and *Sesamia nonagrioides***

104 *Ostrinia nubilalis* originated in Europe and subsequently
 105 invaded parts of Africa, North America, and Eurasia (Dicke
 106 and Guthrie 1988; Capinera 2000; Velasco et al. 2007; Las-
 107 sance 2010). In Europe, and based on biological constants
 108 and climatological data, its northern limit of expansion can
 109 be attributed to latitude 58° N (Keszthelyi and Somfalvi-Toth
 110 2020). In North America, the actual distribution of *O. nubi-*
 111 *lalis* overlaps with most of the maize-producing regions in
 112 the USA (east of the Rocky Mountains) and Canada (Hutch-
 113 erson and Cira 2017; Mason et al. 2018; Keszthelyi and Som-
 114 falvi-Toth 2020). *Ostrinia nubilalis* has been observed in
 115 most of Eurasia as well as in North Africa; however, the
 116 eastern limits of the distribution may be underestimated
 117 (Lassance 2010).

118 The adult longevity of *O. nubilalis* is 18 to 24 days dur-
 119 ing which the females lay their egg masses of 5–50 cream-
 120 colored eggs in an overlapping fish-scale arrangement. Dur-
 121 ing a 14-d oviposition period, the female can lay 400 up to
 122 600 eggs that hatch in 4–9 days (Capinera 2000; McLeod
 123 and Studebaker 2003). Five larval instars are achieved in
 124 about 50 days under field conditions; however, instar dura-
 125 tion varies with temperature. The young larvae prefer to
 126 feed in the whorls of vegetative-stage and on the tassels and

127 upper leaves during the reproductive stages; then larvae
128 enter the leaf midrib, stem, and ear shank causing weakened
129 stalks, ear drop, and restriction of ear and grain develop-
130 ment. *Ostrinia nubilalis* overwinters in a state of diapause at
131 the fifth instar inside the lower portion of the maize stalk, the
132 majority within 30 cm of the soil surface (Schaafsma et al.
133 1996; Hudon et al. 1989). In the spring, the larva spins a
134 cocoon to pupate, which takes 10–12 days. Depending on the
135 environmental conditions, the number of generations varies
136 from 1 to 4 (Capinera 2000; Velasco et al. 2007; Gagnon
137 et al. 2019).

138 *Sesamia nonagrioides* is the major pest in maize-growing
139 areas of the Mediterranean Basin, including Portugal, Spain,
140 Morocco, France, Italy, Greece, Turkey, Middle East, and
141 many countries in Africa (Eizaguirre and Fantinou 2012).
142 In European countries, *S. nonagrioides* can be found up to
143 46° N latitude while its distribution in southern Mediter-
144 ranean countries, such as Morocco, Iran, Syria, and Israel,
145 extended to 31°N (Eizaguirre and Fantinou 2012; Naino Jika
146 et al. 2020).

147 The phenology and biology of *S. nonagrioides* have
148 been reported in detail in several studies (Anglade 1972;
149 Andreadis et al. 2013). The Mediterranean corn borer devel-
150 ops through four main stages: egg, larvae, pupae, and adult,
151 and it overwinters as a diapausing larva in maize stalks and
152 roots difficulting its control by some agronomic practices
153 such as uprooting and exposing the larvae to winter cold
154 (Gillyboeuf et al., 1994, Maiorano et al. 2014). A female of
155 *S. nonagrioides* lays about 200 up to 300 eggs that hatch in
156 5–6 days depending on temperature. For 1–2 days, the young
157 larvae remain grouped and feed on leaf tissue. Larvae then
158 bore galleries into the stems and ears where they spend 25
159 to 30 days and go through 6–7 molts before pupation. The
160 pupal stage takes 12 to 15 days and adults mate right after
161 emergence (Özbek and Hayat 2003). 3–4 generations are
162 completed each year in Greece and Portugal, two to three
163 in Spain, France, and Israel, and four or five in some Medi-
164 terranean regions such as Iran and Turkey (Galichet 1982;
165 Tsitsipis et al. 1984; Cordero et al. 1998; Kayapınar and
166 Kornoşor 1998; Cerit et al. 2006; Velasco et al. 2007).

167 Agronomic and cultural control

168 Agronomic and cultural practices play important roles in
169 regulating pest populations, including intercropping with
170 non-host crops, crop rotation (Khan et al. 1997; Cook et al.
171 2007; Letourneau et al. 2011; Damien et al. 2017), cover
172 crops, tillage practices (Pearsons and Tooker 2017), soil fer-
173 tility, and irrigation management (Han et al. 2019). However,
174 these tactics likely need to be applied on a landscape scale
175 by numerous farmers to have implications for area-wide pest
176 management (Gu et al. 2021). Based on present literature,

177 applied research on agronomic and cultural control mostly
178 targets *O. nubilalis*, with little information regarding *S.*
179 *nonagrioides*.

180 *Intercropping and crop rotation*—In maize, intercrop-
181 ping with soybean does not affect the abundance of *O.*
182 *nubilalis* (Tonhasca and Stinner 1991). However, an ear-
183 lier study showed that maize fields adjacent to potato fields
184 have lower incidence of early season damage by *O. nubilalis*,
185 even though a higher incidence of late-season damage was
186 observed (Umeozor et al. 1986). This finding was attrib-
187 uted to the change in function of intercrops, i.e., the potato's
188 role shifting from trap to nursery crop between *O. nubilalis*
189 generations. In non-maize systems, intercropping practices
190 are also effective in reducing pest abundance, mainly via
191 supporting natural enemy populations. For example, in bell
192 peppers, intercropping with flowering plants has been shown
193 to improve biocontrol of *O. nubilalis* by generalist predators,
194 despite that efficacy may depend on prey density (Bickerton
195 and Hamilton 2012). Moreover, the effectiveness of parasitoid
196 release (e.g., *Trichogramma ostriniae*) could also be
197 improved by intercropping with flowering plants (Russell
198 and Bessin 2009). In maize agroecosystems, multi-year rota-
199 tions significantly reduced *O. nubilalis* abundance because
200 of increased predators abundance compared with no-rotation
201 system (Brust and King 1994). A more recent study has
202 stated that crop rotation does not provide protection against
203 *O. nubilalis* consistently enough to warrant recommendation
204 as a management tactic (Mason et al. 2018).

205 *Cover crops and tillage practices*—Cover crops, which
206 are grown between cash crops, could also provide benefits
207 to cropping systems, including pest control. A recent study
208 showed that the inclusion of winter and interseeded cover
209 crops in organic crop rotations could provide environmen-
210 tal benefits without increasing the risk of damage by insect
211 pests including the *O. nubilalis* (Regan et al. 2020). Yet, this
212 study failed to include a control cropping system in which
213 cover crops were not planted, providing no evidence on the
214 ecological role of cover crops. With a better understanding
215 of the interactions among below-ground and above-ground
216 crop-inhabiting organisms, different cover crop species
217 were found to affect mycorrhizal colonization of subsequent
218 maize roots, which in turn influenced plant nutrient status
219 and herbivory resistance to *O. nubilalis* (Murrell et al. 2020).
220 Compared with a chisel plow and ridge tillage in maize,
221 *Chrysopa* sp. predation of *O. nubilalis* first-generation eggs
222 was highest in no-tillage systems (Andow 1992).

223 *Soil fertility management*—The relationship between
224 mineral fertility and plant susceptibility to insects and dis-
225 ease has been revealed by a considerable body of research.
226 Soil fertility may have an influence on pest incidence via
227 so-called bottom-up effects (Han et al. 2022). Soil fertil-
228 ity status impacted maize mineral balance, which in turn
229 influenced *O. nubilalis* oviposition preference, resulting in

230 differences in egg laying that were nearly 18 times higher
 231 between plants in conventional soil than among those in
 232 organically managed soil (Phelan et al. 1996). Maize root
 233 colonization by arbuscular mycorrhizal fungi (AMF) was
 234 shown to interact with fertilization practices in modifying *O.*
 235 *nubilalis* female oviposition response (Murrell et al. 2015).
 236 The number of eggs oviposited per plant was much lower on
 237 conventionally fertilized plants (36.68 ± 7.04) than on either
 238 standard organically grown plants (70.84 ± 16.10) or plants
 239 with the soil nutrients management based on the basic cation
 240 saturation ratio (BCSR) approach (95 ± 23.41) (Murrell et al.
 241 2015). The oviposition response increased significantly as
 242 AMF colonization increased in organically managed plants
 243 while the opposite effect was observed in BCSR plants.

244 Once the oviposition choice is made, larval performance
 245 is key for *O. nubilalis* population dynamics in the field. Lar-
 246 val development time was affected by the fertilization his-
 247 tory of conventional versus organic maize. *Ostrinia nubilalis*
 248 larvae developed significantly faster on BCSR plants than on
 249 plants under the standard organic approach, with intermedi-
 250 ate development on conventionally fertilized plants (Mur-
 251 rell and Cullen 2014). In that study, the authors concluded
 252 that *O. nubilalis* responded positively to the BCSR maize as
 253 neither larval weight nor survivorship was compromised by
 254 faster development time.

255 Few studies have examined the effects of agronomic and
 256 cultural practices on *S. nonagrioides*. Pest damage could be
 257 minimized when the most susceptible crop stage does not
 258 coincide with peak pest populations. Indeed, early planting
 259 of maize results in the tissues being as mature as possible at
 260 the time of *S. nonagrioides* larval attack, which significantly
 261 reduced pest injury (Ordas et al. 2013). Other agronomic
 262 practices have been shown to be ineffective. For example,
 263 larval density did not vary with irrigation level or fertiliza-
 264 tion regimes (organic versus conventional soil fertilization)
 265 in sweet sorghum (Dimou et al. 2007). Similarly, a modeling
 266 approach providing estimates on the effects of climate warm-
 267 ing on *S. nonagrioides* distribution and development indi-
 268 cated that the agronomic practice of uprooting and exposing
 269 the stubble on the soil surface to cold winter temperatures
 270 may be ineffective for managing the pest (Maiorano et al.
 271 2014).

272 Pheromone-based monitoring and control

273 Both *S. nonagrioides* and *O. nubilalis* emit sex pheromone
 274 blends that comprise typical lepidopteran compounds that
 275 were identified several decades ago. Since then, they became
 276 a model system for basic and applied studies on pheromone
 277 biosynthesis, chemoreception, evolution, and genetics (Mas
 278 et al. 2000; de Santis et al. 2006; Lassance 2010, 2016;
 279 Unbehend et al. 2021). Females of *S. nonagrioides* release a

four-component mixture of Z-11-hexadecenyl acetate (Z11-
 16:Ac), Z-11-hexadecenol (Z11-16:OH), Z-11-hexadecenal
 (Z11:14:Al), and dodecyl acetate (12:Ac) (Sreng et al. 1985;
 Mazomenos 1989; Krokos et al. 2002), while *O. nubilalis*
 female emits a binary blend of (Z)-11-tetradecenyl acetate
 (Z11-14:Ac) and (E)-11-tetradecenyl acetate (E11-14:Ac)
 (Klun et al. 1967; Russell et al. 1975). Their pheromone
 blends are different enough so there is no pheromonal cross-
 attraction among the two species (Gemeno et al. 2006; Cruz
 and Eizaguirre 2016).

Nowadays, pheromone-based commercial products are
 used for monitoring and mating disruption for *O. nubilalis*
 and *S. nonagrioides*. Pheromone-based monitoring allows
 to detect the onset of flight peak and adult emergence of the
 maize borers in crops, so control measures can be applied
 early resulting in more effective population suppression
 (Bažok et al. 2009). Capture of adults in pheromone traps
 associated with egg mass sampling also facilitates timing
 of spraying chemicals, microbial insecticide, or release of
 egg parasitoids to control maize borers. There is also the
 possibility of setting a threshold for the number of adults
 captured to guide control measures. As *O. nubilalis* and *S.*
nonagrioides can have up to four generations depending on
 the environmental conditions (Velasco et al. 2007), phero-
 mone-based monitoring is an important tactic throughout
 the growing season.

Despite the numerous advantages of pheromone-based
 monitoring relative to blacklight traps and scouting fields for
 eggs or injury (Laurent and Frérot 2007), the tactic has some
 drawbacks. Both species exhibit variability in the proportion
 of the pheromone components across populations, making
 this tactic difficult to implement without prior knowledge
 on the pheromone composition of the target population. In
 the case of *S. nonagrioides*, despite variability in the phero-
 mone blend composition emitted by females from different
 geographic populations (Spain, France, and Greece), males
 are attracted to a broad range of pheromone blends (Krokos
 et al. 2002). However, slight changes in the ratio of the com-
 ponents of the synthetic pheromone blend for monitoring *S.*
nonagrioides can enhance efficacy and selectivity in male
 traps in a given location (Mazomenos 1989; Sans et al. 1997;
 Krokos et al. 2002).

In *O. nubilalis*, the dominance of the Z and E geometric
 isomers in the sex pheromone determines two genetic strains
 that exhibit different behavioral and physiological responses
 to Z-11:14:Ac and E-11:14:Ac (Anglade et al. 1984; Glover
 et al. 1987; Dopman et al. 2009; Olsson et al. 2010). The
 most prevalent strain in maize fields is the Z strain, which
 releases the Z and E isomers at 97:3 ratios, while the pro-
 portion is reversed to 1:99 for the E strain, which is often
 associated with many different host crops including hops,
 wheat, peppers, etc. (Klun et al. 1973; Cardé et al. 1975;
 Kochansky et al. 1975). The two *O. nubilalis* pheromone

333 strains can occur sympatrically and eventual crossbreeding
334 results in hybrid individuals that emit a sex pheromone with
335 an intermediary Z/E ratio of 35: 65 (Peña et al. 1988; Glover
336 et al. 1991; Dopman et al. 2009). Thus, as for *S. nonagri-*
337 *oides*, before employing a pheromone-based monitoring
338 strategy for *O. nubilalis* either in Europe or North America,
339 the locally dominant pheromone strain should be considered.

340 Besides the issue of the Z/E ratio in the pheromone blend,
341 trap design and placement have impacted the effectiveness
342 and consistency of pheromone-based monitoring of *O. nubi-*
343 *lalis* (Pelozuelo and Frerot 2006; Laurent and Frérot 2007;
344 Kárpáti et al. 2013). Unlike the monitoring of several moth
345 pests in which the delta trap is used, the most appropriate
346 trap design for monitoring *O. nubilalis* is the nylon or wire-
347 mesh cone trap (also known as the *Heliothis* trap), which
348 traps up to six times more adults than delta traps (Pelozuelo
349 and Frerot 2006; Kárpáti et al. 2013). Moreover, captures
350 of *O. nubilalis* males in pheromone-baited cone traps are
351 optimized when they are placed within the maize canopy
352 instead of above it (Mason et al. 1997). The many factors
353 that influence moth catches in pheromone-baited traps, such
354 as those presented, are not always given as instructions by
355 manufacturers, hence making this tactic less efficient.

356 Although pheromone-based monitoring of *S. nonagri-*
357 *oides* has been far less studied than that of *O. nubilalis*
358 (Mazomenos 1989; Sans et al. 1997; Ameline and Frérot
359 2001), the method for *S. nonagrioides* mating disruption has
360 advanced further (Perdiguer et al. 1992). For monitoring,
361 the four-component blend of *S. nonagrioides* is necessary
362 to selectively capture males, and depending on the locality
363 the component ratio in the blend is different as previously
364 mentioned (Mazomenos 1989; Sans et al. 1997; Ameline
365 and Frérot 2001; Albajes et al. 2002). Mating disruption of
366 *S. nonagrioides*, measured in terms of reduction of popula-
367 tion density between generations in treated and untreated
368 areas, has been tested using either the full pheromone blend
369 or a simplified blend comprising the two major components
370 (Frérot et al. 1997; Albajes et al. 2002). Interestingly, the
371 simplified pheromone blend at high concentrations not only
372 works for suppressing *S. nonagrioides* population, but also
373 of *O. nubilalis* (Albajes et al. 2002; Eizaguirre et al. 2002).
374 The reduction of *O. nubilalis* population in areas treated
375 with *S. nonagrioides* pheromone does not result from mating
376 disruption as the two maize borers do not share pheromonal
377 components, but from an inhibition response of males being
378 attracted to their own sex pheromone (Eizaguirre et al. 2002;
379 Gemeno et al. 2006; Linn et al. 2007). A similar antagonistic
380 effect is observed when *S. nonagrioides* males are exposed
381 to *O. nubilalis* sex pheromone in both the laboratory and
382 field (Eizaguirre et al. 2007, Lopez-Alonso et al. 2011). This
383 cross-inhibition effect using either maize borers' pheromone
384 blend makes mating disruption a promising behavioral strat-
385 egy to suppress both pests.

Besides pheromones, other semiochemicals of varying
effects (e.g., pheromone analogs and plant volatiles) have
also been proposed for manipulating the behavior of the
maize borers in the field. Sole et al. (2007) found that
(Z)-11-hexadecenyl trifluoromethyl ketone (an antagonist
analogue of the pheromone of *S. nonagrioides*) was effec-
tive in reducing damage caused by second and third gener-
ations of *S. nonagrioides* and *O. nubilalis*. More recently,
a non-pheromone lure to capture male and female *O. nubi-*
lalis has been developed. The well-known lepidopteran
attractant phenylacetaldehyde, a floral volatile, when com-
bined with 4-methoxy-2-phenethyl alcohol increased the
capture of *O. nubilalis* individuals three- to fivefold com-
pared to the attractant alone (Tóth et al. 2016). Because
this lure traps both sexes, it has the potential for being
used in the mass-trapping of *O. nubilalis*.

Although at initial laboratory experimental stages, host
volatile emissions have been investigated as a source of
attractants to *O. nubilalis* and *S. nonagrioides* females, and
may be used in the future in lures for monitoring or mass-
trapping tactics. For gravid female *O. nubilalis* (Z strain),
nonanal, decanal, and methyl salicylate, which are volatile
organic compounds (VOCs) emitted by maize plants, con-
sist of important cues to identify the host plant, and the
mixture of nonanal and decanal seems to be promising to
capture females in the field (Solé et al. 2010, Mólnar et al.
2015). These two aldehydes are also biologically active
compounds for *S. nonagrioides*; however, they act as ovi-
position deterrents when tested individually (Konstanto-
poulou et al. 2004). At last, another approach to exploiting
plant volatiles is the inoculation of microorganisms that
promote plant growth at the same time that they elicit or
prime plant chemical defenses, often resulting in a distinct
VOC profile (Pereira et al. 2021). Disi et al. (2018) tested
this management strategy in *O. nubilalis*-maize system
under laboratory conditions, and showed that seed inocula-
tion with the rhizobacteria *Bacillus pumilus* reduces VOC
emission of maize plants, making them less attractive to
moths.

After more than three decades from the identification of
the sex pheromone of the two corn borers, formulation of
pheromone-based monitoring for both pests has been made
viable after understanding the variability in the sex phero-
mone blend across populations. In contrast, development
of a commercial product for mating disruption of the corn
borers is at initial stages. The synthesis of large quantities
of their pheromone compounds is still expensive, and a tech-
nology that release them at constant rates for weeks in the
field is needed (Albajes et al. 2002; de Vlieger 2008). Novel
and less costly methods for scaling up the synthesis of phero-
mone components of *O. nubilalis* have been investigated
and may make mating disruption a less costly tactic in the
future (Petkevicius et al. 2021).

439 Biological control using predators 440 and parasitoids

441 To reduce pests, biological control using natural enemies
442 such as predators and parasitoids has been developed. It is an
443 eco-friendly and efficient integrated pest management tactic
444 that generally has no negative effects (Dreistadt 2007).

445 *Trichogramma* spp. parasitoids have been used for over
446 100 years as biocontrol agents against many lepidopteran
447 pests and are widely used in Europe for inundative and aug-
448 mentative release against *O. nubilalis* (Bigler and Brunetti
449 1986; Ravensberg and Berger 1988; Hassan 1993; Pavlík
450 1993; Hassan and Wajnberg 1994) (Table 1). In China,
451 France, Germany, Moldova, and Turkey, *Trichogramma*
452 *ostriniae* (Russell and Bessin 2009) and *T. evanescens*
453 (Westwood) have been found to be the most effective species
454 for controlling *O. nubilalis* (Özpinar et al. 1999). Several
455 *Trichogramma* spp. continue to be commercially available
456 for biological control worldwide (Smith 1996; Pinto 1999;
457 Consoli et al. 2010). Besides being easily and quickly pro-
458 duced, they are also effective at controlling pest eggs and
459 minimizing subsequent larval injury (Smith 1996; Mansour
460 2010; Mills 2010). Therefore, *Trichogramma* species should
461 continue to be considered as an augmentation approach for
462 effective biological control against *O. nubilalis*.

463 In the USA, *Trichogramma ostriniae* has also been identi-
464 fied as a potential biological control agent for *O. nubilalis*
465 (Hoffmann 1997; Wang et al. 1999; Wright et al. 2001) but

466 because even low levels of insect feeding on sweet corn ears
467 render the product unusable, previous attempts to improve
468 *O. nubilalis* biological management using this parasitoid
469 have largely failed (Hoffmann et al. 1996). In fact, although
470 the released *T. ostriniae* adults were effectively established
471 during each season and increased *O. nubilalis* larval mortal-
472 ity by 61–93% (Kuhar et al. 2002), they were found unable to
473 overwinter in the USA (Hoffmann et al. 2002) and the control
474 provided was affected by extreme high and low tempera-
475 tures (Wang et al. 1997). Additionally, inundative releases
476 of indigenous *Trichogramma* spp. such as *T. evanescens*,
477 *T. brassicae* Bezdenko and *T. nubilale* Ertle and Davis for
478 the biological control of *O. nubilalis* have shown variable
479 results (Losey et al. 1995; Mertz et al. 1995; Smith 1996).
480 The effect of indigenous natural enemies alone on *O. nubila-*
481 *lis* was insufficient to reduce economic damage (Wright et al.
482 2002) and is mostly compromised by insecticide applications
483 (Pimentel and Andow 1984). Furthermore, the inundative
484 approach is relatively costly and not always effective, as
485 releases must be carefully timed to maximize their effect.
486 Inoculative releases, in contrast, involve the introduction of
487 a small number of parasitoids early in the season and rely on
488 their successful establishment in the crop for control later in
489 the season. Because the parasitoid population is established
490 early in the season and allowed to track changes in the tar-
491 get pest population, rather than acting as a cure option, this
492 approach should be less sensitive to timing constraints as in
493 the case of inundative releases (Hoffmann et al. 2002).

Table 1 Reported egg parasitism rates, larval infestation, and plant damage reduction for different *Trichogramma* species assessed for the control of *Ostrinia nubilalis* and *Sesamia nonagrioides*

Species	Reported egg parasitism, larval infestation, or plant damage reduction	Region or country	References
<i>Trichogramma</i> spp.	Egg parasitism: 86.8–96.2%	France	Voegele et al. (1975)
<i>T. evanescens</i>	Egg parasitism: 100%	Northern Switzerland	Bigler and Brunetti (1986)
	Egg parasitism: 96%	Black Sea region, Turkey	Özdemir (1981)
	Reduced infestation from 68.3–95.2% to 4.0–5.6%		Suter and Babler (1976)
	Natural rates of egg parasitism: from 2.4 to 51.1%	Cukurova, Turkey	Kayapinar (1991)
	Egg parasitism: up to 75.5%	Cukurova, Turkey	Kayapinar (1991), Özpinar and Kornoşor (1997)
	Egg parasitism: 80.93% and reduction of the larval infestation to 57.14% in infested plants	Mediterranean region of Turkey	Kornoşor et al. (1995a, b)
	Natural egg parasitism: between 87.2 and 98.6%	Western Black Sea region, Turkey	Melan et al. (1996)
<i>T. maidis</i>	Reduced plants damages by 96%	Turkey	Oztemiz (2009)
	Egg parasitism: 87%	Bulgaria	Karadjov (1989)
<i>T. ostriniae</i>	Inundative release reduced the larval attack by about 70%	Switzerland	Bigler and Brunetti (1986)
	Egg parasitism: 34.4–48.7%	USA	Kuhar et al. (2002, 2004)
	Egg parasitism: 14.9–15.3%	Kentucky, USA	Friley (2004)
	Egg parasitism: 4–6%	Kentucky, USA	Russell and Bessin (2009)
	Plant damage was reduced by about 50%	New York, USA	Wright et al. (2002)
Egg parasitism: 70–90%	Massachusetts, USA	Wang et al. (1997)	

494 Other parasitoids of *O. nubilalis* include many species
495 of Hymenoptera (i.e., Braconidae; Eulophidae; Ichneumo-
496 nidae) and Diptera (Tachinidae). Additionally, numerous
497 generalist predator species have been reported to be effective
498 for biological control of *O. nubilalis*, including those
499 from various Coleoptera (Coccinellidae, Staphylinidae, etc.),
500 Hemiptera (Anthocoridae, Pentatomidae, Reduviidae, etc.),
501 Neuroptera (Chrysopidae), Dermaptera (Anisolabididae),
502 Orthoptera (Acrididae), and some acari (Trombidiidae,
503 Erythraeidae) families, have been reported to be success-
504 ful in controlling *O. nubilalis* biologically (Supplementary
505 Table 1). However, the potential use of these parasitoids and
506 predators at large scale and under field conditions for the
507 management of *O. nubilalis* is still to be confirmed.

508 One of the most effective biocontrol agents of *S. nona-*
509 *agrioides* is *Telenomus (Platytenomus) busseolae* Gahan
510 (Hymenoptera: Scelionidae), a solitary egg parasitoid of
511 many lepidopteran pests (Alexandri and Tsitsipis 1990;
512 Setamou and Schulthess 1995). The geographic distribu-
513 tion of this parasitoid covers all of Africa, the Middle East,
514 India, Iran, Iraq, Israel, Greece, and Turkey (Kayapınar
515 and Kornoşor 1990; Polaszek et al. 1993). Many research-
516 ers have confirmed the efficiency of *T. busseolae* as an egg
517 parasitoid of maize borers (Bayram et al. 2005; Jamshidnia
518 et al. 2010).

519 The *T. busseolae* parasitism of *Sesamia* sp. eggs was
520 found to range from 60 to 80% on sugarcane in Ghana
521 (Scheibelreiter 1980). *Telenomus busseolae* was found to
522 be associated with 60–80% of *S. nonagrioides* egg masses in
523 the Mediterranean region of Turkey (Kornosor et al. 1995).
524 Similar results were reported in Greece by Alexandri and
525 Tsitsipis (1990).

526 Other parasitoids of *S. nonagrioides* include species from
527 the Hymenoptera (i.e., Braconidae; Eulophidae; Ichneumo-
528 nidae; Pteromalidae; Scelionidae) and Diptera (Tachini-
529 dae; Sarcophagidae). In addition, many generalist predator
530 species have been shown to effectively control *S. nonagri-*
531 *oides*, including species from Coleoptera (Coccinellidae),
532 Hemiptera (Anthocoridae; Miridae; Nabidae; Lygaeidae),
533 Neuroptera (Chrysopidae), and some acari (Trombidiidae)
534 (Supplementary Table 2).

535 Parasitoids of the genera *Trichogramma* spp. and *Tel-*
536 *enomus* spp. can be considered the most promising natural
537 enemies to be used in applied biological control of stem bor-
538 ers within IPM systems, especially because of their recog-
539 nized efficacy as biocontrol agents worldwide, and available
540 methodologies for mass rearing. Furthermore, these parasit-
541 oids target the egg stage which is beneficial as the control is
542 achieved before the larval stage that is harmful to the plant.
543 Therefore, devising compatible management strategies to
544 optimize their efficacy is highly encouraged. For instance,
545 identifying and releasing the most adapted parasitoid species
546 (e.g., *T. ostrinae*, *T. evanescens*, *T. brassicae*, or *T. nubilale*

547 in the case of *O. nubilalis*) in each production region should
548 provide higher levels of control (Losey et al. 1995; Mertz
549 et al. 1995; Smith 1996; Gagnon et al. 2017). Evaluation of
550 insecticides registered for stem borer control regarding their
551 selectivity is also necessary to be harmoniously integrated
552 with biological control (Vasileiadis et al. 2017). In addi-
553 tion, the frequency and number of parasitoids to be released
554 in the field (Murali-Baskaran et al. 2021) are to be opti-
555 mized for each targeted pest and environmental conditions.
556 Finally, synergism between plant kairomones, pheromones,
557 and parasitoids through changes in previous experience and
558 behavior of the natural enemy should improve foraging effi-
559 ciency and biocontrol in the field, as already reported for
560 related insect species (Tognon et al. 2020), meriting further
561 investigations for stem borers.

562 Microbial control

563 Entomopathogenic nematodes

564 Entomopathogenic nematodes (EPNs) have recently
565 attracted attention in plant protection as a biological control
566 agent that can be commercially produced and used for soil-
567 inhabiting insects (Gaugler 1981; Klein 1990; Smart 1995;
568 Canhilal et al. 2017). Approximately 3000 insect-nematode
569 associations have been reported, covering 19 insect orders
570 and 14 EPNs families (Kaşıkavalcı 1999). Juvenile EPNs
571 penetrate the body cavity of insects either through natural
572 body openings such as the anus, mouth, respiratory system,
573 and genital pore or by penetrating the insect cuticle. EPNs
574 from the Heterorhabditidae and Steinernematidae families,
575 including (Gaugler 1981; Kaya and Gaugler 1993) *Stein-*
576 *ernema* (Rhabditida: Steinernematidae) and *Heterorhabditis*
577 (Rhabditida: Heterorhabditidae) species, are mutually asso-
578 ciated with *Xenorhabdus* spp. and *Photorhabdus* spp. bacte-
579 ria, respectively. Consequently, the mutualistic relationship
580 results in bacteria rapidly multiplying and causing the death
581 of the insect host within 24–48 h (Kaya and Gaugler 1993;
582 Berry 2007).

583 *Steinernema glaseri* or *S. feltiae* were shown to protect
584 maize plants against *O. nubilalis* under laboratory and
585 greenhouse conditions (Riga et al. 2001). *Steinernema car-*
586 *pocapsae* similarly caused high mortality of *O. nubilalis*
587 larvae in the greenhouse (Ben-Yakir et al. 1998).

588 To the best of our knowledge, the potential of EPNs for
589 the control of *S. nonagrioides* has not been investigated
590 so far. However, Halawa et al., (2007) noted that *S. car-*
591 *pocapsae* caused between 60 and 73% mortality of *S. cre-*
592 *tica* depending on their inoculation density. Furthermore,
593 Gözel and Güneş (2013) determined the virulence of three
594 Turkish strains of the entomopathogenic nematodes *H. bac-*
595 *teriophora*, *S. feltiae*, and *S. carpocapsae* on *S. cretica* last

instars under different temperatures (15, 20, 25, and 30 °C). They reported similar mortality among the three strains at all applied temperatures and their effectiveness increased as temperature increased. Mortality of *S. cretica* exposed to *S. carpocapsae*, *S. feltiae*, and *H. bacteriophora* reached 82, 90, and 90% at 25 °C, respectively.

Entomopathogenic fungi

With over 28 species, the genus *Beauveria* is one of the most common and widely used entomopathogenic fungi in plant protection. Application of *B. bassiana* against *O. nubilalis* larvae dates back to the 1920s (Metalinkov and Toumanoff 1928). The potential of different isolates of *Beauveria* to control *O. nubilalis* populations when used as a biopesticide has been previously investigated (Safavi et al. 2010; Medo et al. 2021), although previous bioassays indicated that *B. bassiana* loses virulence against *O. nubilalis* once the pest colonizes maize (Wagner and Lewis 2000). Mortality of 4th instars ranging from 34 to 96% at a concentration of 10⁷ conidia ml⁻¹ has been reported in a screening of 46 soil isolates of *Beauveria* spp. against *O. nubilalis* (Medo et al. 2021). Field-collected strains of *B. bassiana* were reported to be virulent to *O. nubilalis* larvae at a concentration of 4.8 × 10⁵ conidia ml⁻¹ (Demir et al. 2012). Moreover, *B. bassiana* reduced tunneling by *O. nubilalis* from between 10.07 and 3.24 cm per plant in untreated maize plants to less than 0.69 cm per plant in the *B. bassiana*-treated plants (Bing and Lewis 1992). Maize borer infestation was significantly reduced in plots with *B. bassiana*-treated plants (less than 21%) compared to untreated plots (over 97%) under field conditions (Sabbour et al. 2011).

Interactions between the entomopathogenic bacterium *Bacillus thuringiensis* (Bt) *ssp.* *kurstaki* and two entomopathogenic fungi, *B. bassiana* and *Metarhizium robertsii*, against *S. nonagrioides* larvae were evaluated with laboratory bioassays (Mantzoukas et al. 2015). A positive interaction between pathogens was observed, leading to mortality between 54 and 100% at 16 days of larval exposure to a combination of either fungus with the entomopathogenic bacterium.

The same authors (Mantzoukas et al. 2015, 2020) investigated the entomopathogenic action of three fungal endophytes, *B. bassiana* (Balsamo), *M. robertsii*, and *Isaria fumosorosea*, against *S. nonagrioides* larvae artificially introduced into *Sorghum bicolor* L. plants under natural conditions. They reported that the fungi efficiently induced the mortality of larvae, reduced their relative growth rate, and feeding performance. They also noted that the entomopathogens prevented 50–70% of larvae from entering stalks, caused larval mortality ranging from 70 to 100%, and reduction of tunnel lengths by 60–87%.

Entomopathogenic bacteria

Over the last 25 years, researchers, industry, and farmers have become increasingly interested in entomopathogenic bacteria as a form of biological control (ISCCCA 29,021). *Bacillus thuringiensis* (Berliner) (Bt) is the most commonly used entomopathogenic bacterium. It is gram-positive, aerobic, spore-forming, and produces crystals containing specific insecticidal endotoxins (Cry proteins) (Rui et al. 2013). Cry endotoxins act in the insect midgut via a pore-forming mechanism, causing damage to the epithelium (Pigott and Ellar 2007). Several Cry toxins are classified by their spectrum of activity. Primary Cry proteins for maize pests include Cry1, Cry2, and Vip3A for lepidopteran species, and Cry3 for coleopteran species (Schnepf et al. 1998). Most of the scientific community and industry efforts have been focused on Bt among the entomopathogenic bacteria for its ease of use, efficiency, low production cost, considerable diversity of toxins, and lack of toxicity to humans and non-target organisms (Sanchis and Bourguet 2008).

Bt first became available as a commercial bioinsecticide in France in 1938 where it was used to manage *O. nubilalis* damage in maize fields via foliar application (Aronson et al. 1986). Laboratory bioassays using pure Cry1Ab endotoxin from Bt to establish baseline susceptibility of *O. nubilalis* and *S. nonagrioides* have indicated that *S. nonagrioides* is at least as susceptible to this toxin as *O. nubilalis* (González-Núñez et al. 2000). According to Eski et al. (2015), Bt and *B. safensis* caused 93 and 80% mortality in *S. nonagrioides* larvae, respectively. However, the most widespread and successful application of Bt was achieved with the introduction of genetically engineered crops (see Bt technology and varietal resistance section).

Microsporidia

Microsporidia are widespread and persistent entomopathogens with integrated pest management implications. A few of them are considered as potential biocontrol agents (Lewis et al. 2009; Zimmermann et al. 2016; Malysh et al. 2021). Several species of microsporidia are highly virulent to insects with reported regulatory effects on populations of lepidopterans. The microsporidium *Nosema pyrausta* Paillet (Microsporidia: Nosematidae) is an obligate intracellular parasite that can negatively affect the biology of *O. nubilalis*. The pathogen is maintained in a population by horizontal transmission to other host individuals and by vertical transmission to the progeny via infected eggs.

This microsporidium was found frequently in larvae and adults of *O. nubilalis* in maize-growing regions of France, Italy, Hungary, Germany, Slovakia, the Czech Republic, Serbia, and Russia (Zimmermann et al. 2016). In the USA, Lewis et al. (2006) determined the establishment and

696 behavior of *N. pyrausta* in a natural *O. nubilalis* population
 697 in an extensive six-year field study. *Nosema pyrausta* causes
 698 chronic infections leading to slowed larval development and
 699 increased larval mortality. Depending on the intensity of the
 700 infection and the age of the host, it can extend time to pupa-
 701 tion, decrease adult longevity, female oviposition, and fecun-
 702 dity (Lewis et al. 2009; Zimmermann et al. 2016). *Nosema*
 703 *pyrausta* has been reported to cause depression of insect host
 704 populations (Lewis et al. 2009; Zimmermann et al. 2016)
 705 and is suspected of inducing female-biased sex ratios in low-
 706 density populations of *O. nubilalis* (White et al. 2014). The
 707 6- to 8-year periodicity of *O. nubilalis* populations in the
 708 USA has been attributed to this pathogen (Hutchison et al.
 709 2010). In China, besides *N. pyrausta*, its related species *N.*
 710 *furnacalis* is also present (Zimmermann et al. 2016). No
 711 association between this pathogen and *S. nonagrioides* has
 712 been reported up to now.

713 Microbials are generally considered desirable options for
 714 pest management, but their potential to control *O. nubila-*
 715 *lis* and *S. nonagrioides* remains largely neglected and less
 716 explored. Overall and despite the increased research on
 717 microbials as potential biopesticides, only limited quanti-
 718 ties of microbial biopesticides have been produced. Some of
 719 the already commercialized microbial-based biopesticides,
 720 like the bacterium *B. thuringiensis* and the fungi *B. bassiana*
 721 and *M. robertsii*, with proven activity against other lepidop-
 722 teran pests, might be tested and used, alone or in combina-
 723 tion, in corrective applications against the two stem borers.
 724 Depending on the target pest and the mechanism of action,
 725 microbial-based biopesticides can be applied as foliar sprays,
 726 root dips, soil amendments, seed treatments, or a combina-
 727 tion of different methods. However, as for the control of
 728 other pests, the efficacy of such products will continue to
 729 suffer from some limitations. Under field conditions, envi-
 730 ronmental factors like high temperatures and UV radiation
 731 heat might be detrimental to the viability and infectivity of
 732 the applied microbial agent. With the advent and the use of
 733 new technologies like micro-encapsulation, specific formu-
 734 lations could be developed to enhance the efficiency and
 735 tolerance of microbial against adverse environmental effects.

736 Biotechnological controls

737 Varietal resistance and Bt technology

738 In the twentieth century, conventional breeding for resist-
 739 ance to corn stemborers began. In the mid 1950s, the first
 740 recurrent selection program to improve maize resistance
 741 against the first generation of *O. nubilalis* was initiated in the
 742 USA (Penny et al. 1967). That pioneer recurrent selection, as
 743 well as subsequent recurrent selections, significantly reduced
 744 *O. nubilalis* leaf and/or sheath-collar damage but did not

745 improve resistance to stem damage caused by the second
 746 generation; in the meantime, some agronomic traits, such
 747 as yield or precocity, were negatively correlated with plant
 748 resistance (Penny et al. 1967; Russell et al. 1979; Tseng et al.
 749 1984; Klenke et al. 1986; Nyhus et al. 1988). Afterward,
 750 inbred lines with partial resistance to *O. nubilalis*' first gen-
 751 eration were obtained through pedigree selection or back-
 752 crossing (Abel et al. 2000; Willmot et al. 2005).

753 As researchers began to emphasize the importance of
 754 developing materials that were resistant to both generations
 755 of *O. nubilalis*, recurrent and pedigree selection programs
 756 were re-oriented resulting in the successful release of mate-
 757 rials that were resistant to both generations (Russell and
 758 Guthrie 1982; Barry et al. 1983, 1995; Hawk 1985; Dicke
 759 and Guthrie 1988). Nonetheless, selection for increased
 760 resistance appeared to be associated with lower yield, so
 761 new efforts were focused on selection for tolerance, defined
 762 as the plants' ability to reduce yield loss when attacked by
 763 insects. Recurrent selection for tolerance to *O. nubilalis*
 764 resulted in yield increases of 0.49 Mg ha⁻¹ for uninfested
 765 plots and 0.74 Mg ha⁻¹ for infested plots; meanwhile, 63
 766 flint and dent inbred lines, adapted to European conditions,
 767 with high-yielding feature and appreciable levels of *O. nubi-*
 768 *lalis* tolerance were developed and released (Anglade 1972;
 769 Panouillé et al. 1998).

770 At the beginning of the XXI century, Bt hybrids began
 771 to be seen as the final solution for maize stemborer control
 772 and breeding programs for increasing maize natural resist-
 773 ance and tolerance to *O. nubilalis* were almost closed in
 774 the USA and Europe. However, as marker-assisted selection
 775 (MAS) was also seen as a promising alternative to conven-
 776 tional breeding, some quantitative trait loci (QTL) studies
 777 for resistance to *O. nubilalis* were developed, but no MAS
 778 programs based on those results have been carried out,
 779 although it has been empirically demonstrated that MAS
 780 can be effective in selecting for resistance to *O. nubilalis*
 781 (Jampatong et al. 2002; Flint-Garcia et al. 2003; Cardinal
 782 et al. 2006; Orsini et al. 2012; Foiada et al. 2015).

783 On the other hand, selection programs for improving
 784 maize resistance and/or tolerance to stalk tunneling by *S.*
 785 *nonagrioides* larvae have been ongoing since the 1920s
 786 at the Misión Biológica de Galicia (CSIC, Spain). Intra-
 787 populational and reciprocal recurrent programs as well as
 788 pedigree selection for inbred development were successful
 789 in reducing stem tunnel lengths by *S. nonagrioides* larvae or
 790 increasing yield under high insect pressure (Sandoya et al.
 791 2008; Samayoa et al. 2012; Ordas et al. 2013; Butrón et al.
 792 2014). However, as it was observed in breeding for resist-
 793 ance to *O. nubilalis*, resistance to stem tunneling by *S. nona-*
 794 *grioides* and yield are often negatively correlated (Butrón
 795 et al. 2012). Therefore, MAS selection was envisioned as an
 796 alternative to phenotypic selection once genetic factors for
 797 resistance and yield could be disentangled. QTL studies for

798 maize resistance to stem tunneling by *S. nonagrioides* larvae
 799 were carried out and MAS selection based on DNA markers
 800 flanking some QTLs was proven suitable to improve resist-
 801 ance without detrimental effects on yield (Ordas et al. 2009,
 802 2010, 2013; Samayoa et al. 2014, 2015a, 2015b, 2019; Jimé-
 803 nez-Galindo et al. 2017, 2019). Nowadays, genomic selec-
 804 tion is preferred over MAS selection approaches when traits
 805 are controlled by many genes with small additive effects as
 806 is the case for maize resistance and tolerance to stemborer
 807 attack. In this scenario, genomic selection for yield under
 808 *S. nonagrioides* infestation was useful to simultaneously
 809 increase yield and resistance to stem tunneling (paper in
 810 preparation).

811 Simultaneously to direct selection programs to improve
 812 resistance to stem borers, selections for the DIMBOA
 813 (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-ona) content
 814 and for pith cell-wall strengthening were carried out to indi-
 815 rectly improve resistance to leaf feeding and stem tunneling,
 816 respectively. Those indirect selection approaches were suc-
 817 cessful for developing maize varieties with increased resist-
 818 ance, probing that hydroxamic content of the leaf-whorl
 819 and pith cell-wall strength are important components of
 820 resistance to the first and second generations of stem bor-
 821 ers, respectively (Russell et al. 1975; Barros-Rios et al.
 822 2015). Rodriguez et al. (2021) recently reported that levels
 823 of resistance in the field should depend on induced defense
 824 responses of maize plants infested by *S. nonagrioides* rather
 825 than on constitutive resistance levels, evaluating the con-
 826 centrations of candidate metabolites that may be involved.
 827 Therefore, specific methodologies for evaluation of induced
 828 plant resistance on stem borer biological performance are
 829 needed, as well as the quantification of those potential sec-
 830 ondary compounds underlying induced resistance, which
 831 could be added as a complementary control method in IPM
 832 systems, especially where transgenic *Bt* hybrids are not
 833 allowed or in organic agriculture.

834 Although many maize varieties with partial resistance
 835 to *O. nubilalis* and *S. nonagrioides* attack have been deliv-
 836 ered through decades of maize breeding for resistance and/
 837 or tolerance to attack by these insects, these materials have
 838 been underused because they cannot compete with the
 839 total resistance of *Bt* hybrids. The use of biotechnology
 840 and genetic engineering techniques in the development of
 841 new plant varieties began at the end of the XX century and
 842 has meant an enormous advance in pest control with the
 843 appearance of insect-resistant transgenic crops or *Bt* crops,
 844 which incorporate genetic material from *Bt* in their genome.
 845 As mentioned above, *Bt* has insecticidal properties due to
 846 the production of Cry (crystal) and Cyt (cytolytic) insec-
 847 tical proteins produced during the sporulation phase of
 848 the bacterium, and Vip (vegetative insecticidal proteins)
 849 produced during the vegetative growth phase (Bravo et al.
 850 2017; Terenius et al. 2011). Currently, Cry proteins are the

851 active ingredient in the vast majority of genetically modi-
 852 fied (GM) maize hybrids for the control of *O. nubilalis* and
 853 *S. nonagrioides* (Hutchison et al. 2010; Huang et al. 2011).
 854 The great advantage of *Bt* maize in the control of maize bor-
 855 ers compared to conventional chemical insecticides is that
 856 the toxin is expressed in plant tissues throughout the crop
 857 cycle, protected from UV radiation, and provides maize with
 858 inherent resistance to the pests. In this way, maize-boring
 859 larvae, which are not usually accessible to insecticides as
 860 most of their larval cycle takes place inside the maize stalk,
 861 are killed when they feed on the plant. *Bt* maize has sig-
 862 nificantly reduced the occurrence of *O. nubilalis* in North
 863 America, shown excellent yield protection from this pest,
 864 and reduced the infection of secondary mycotoxigenic fungi
 865 (Schaafsma et al. 2002; Hutchison et al. 2010; Dively et al.
 866 2018; Pellegrino et al. 2018). Finally, it has been shown that
 867 varieties expressing Cry proteins for maize borer control
 868 have no significant negative effects on non-target arthropods
 869 present in the crop (Daly and Buntin 2005; Farinós et al.
 870 2008; Higgins et al. 2009; Lopez et al. 2011; Arias-Martín
 871 et al. 2016, 2018). For these reasons, *Bt* maize is considered
 872 a suitable tool in integrated pest management strategies and
 873 has been widely adopted (Kennedy 2008). However, there is
 874 still great social rejection in many countries due to a number
 875 of reasons. These include the public's unfamiliarity with bio-
 876 technology and agriculture and misconceptions about GM
 877 technology (Huesing et al. 2016). Particularly in the case of
 878 the EU, this rejection is based on political considerations
 879 rather than scientific principles (Davison 2010).

880 In 1996 and 1997, the first transgenic maize was com-
 881 mercialized in the USA and Canada, respectively, expressing
 882 a high dose of Cry1Ab targeting *O. nubilalis* (Ostlie et al.
 883 1997; Marçon et al. 1999). Cultivation of *Bt* maize express-
 884 ing Cry1Ab spread rapidly in North America. Cry1Ab maize
 885 was first grown in Europe in 1998 for the control of *O. nubi-*
 886 *lalis* and also *S. nonagrioides*, which proved to be very effec-
 887 tive (Farinos et al. 2004), being also highly efficient in the
 888 reduction of mycotoxigenic fungi (Arias-Martín et al. 2021).
 889 Since then, a number of transgenic maize events incorporat-
 890 ing Cry1Ab or other *Bt* toxins, alone or in combination (sin-
 891 gle or pyramided events), have been successfully developed
 892 and marketed for the control of *O. nubilalis* and other pests
 893 (ISAAA 2021). Currently, there are five *Bt* proteins pro-
 894 duced from various maize events targeting lepidopteran pests
 895 in North America: Cry1Ab, Cry1Fa, Cry1A.105, Cry2Ab2,
 896 and Vip3A (DiFonzo 2021). *Ostrinia nubilalis* has proven
 897 to be susceptible to these Cry toxins (Tan et al. 2013), but is
 898 not susceptible to Vip3A (Hernández-Rodríguez et al. 2013;
 899 ISAAA 2021). As for *S. nonagrioides*, it has been shown to
 900 be highly susceptible to the Cry1Ab toxin expressed in MON
 901 810 maize, the only *Bt* maize approved so far for cultivation
 902 in the EU. At present, the only European countries growing
 903 MON 810 maize are Spain and Portugal, but only in Spain

904 have these hybrids been continuously commercialized on a
905 large scale (Albajes et al. 2012; Farinós et al. 2018). Never-
906 theless, laboratory studies have revealed that *S. nonagrioides*
907 is also susceptible to other Cry toxins (González-Cabrera
908 et al. 2006) and to TC1507 maize event expressing Cry1F,
909 which was shown in feeding trials to cause mortality equiva-
910 lent to that obtained with a maize hybrid expressing Cry1Ab
911 (Farinós et al. 2011; Albajes et al. 2012).

912 One of the main threats to the long-term sustainability of
913 *Bt* crops is the evolution of resistance in target pest popula-
914 tions to the insecticidal proteins as large-scale cultivation,
915 continuous exposure to Bt proteins, and the use of transgenic
916 events expressing proteins with the same action mechanism,
917 represent strong selection pressure for resistance (Tabashnik
918 et al. 2009; Tabashnik and Carrière 2017). For this reason,
919 insect resistance management (IRM) programs have been
920 developed with the aim of maximizing product lifespan
921 and delaying the development of target pest resistance to
922 *Bt* maize (Head and Greenplate 2012). The most generally
923 recommended and widely adopted IRM strategy for maize
924 borers is known as “high dose/refuge” (HDR). This strategy
925 is based on the use of varieties with a high dose of *Bt* toxin
926 against the target pest and on the establishment of non-*Bt*
927 plants that act as refuge for insects that are susceptible to
928 the toxin (Siegfried and Hellmich 2012). The expression
929 of high doses of *Bt* toxins allows both susceptible (SS) and
930 heterozygous resistant (RS) individuals to be controlled by
931 feeding on the plant. The refuge functions as a source of
932 susceptible insects to mate with the homozygous resistant
933 (RR) insects that may emerge from the *Bt* field. Refuges are
934 planted either as structured blocks or strips within or close
935 to the *Bt* field or integrated throughout the field by planting
936 blended seed lots (also called refuge-in-the-bag (RIB) or
937 integrated refuge) (Yang et al. 2015). In addition, the combi-
938 nation (pyramiding) of multiple *Bt* toxins in the same hybrid
939 is intended to further delay the possible emergence of pest
940 resistance more effectively than using individual *Bt* toxins
941 (Carrière et al. 2015).

942 The HDR resistance management strategy has proven
943 to be very successful in maintaining the susceptibility of
944 *O. nubilalis* and *S. nonagrioides* to *Bt* toxins (Huang et al.
945 2011; Terenius et al. 2011; Castañera et al. 2016). No field
946 control failures have been reported for either species in Ibe-
947 rria after more than 20 years of commercial use of Cry1Ab-
948 expressing MON810 maize, as evidenced by monitoring
949 programs carried out to detect early changes of susceptibil-
950 ity in field insect populations (Farinós et al. 2018; Thieme
951 et al. 2018). However, a recent study has concluded that the
952 frequency of resistance alleles of *S. nonagrioides* in the Ebro
953 valley, an important maize-growing region in Spain, is now
954 triple the value recommended for effective implementation
955 of the HDR strategy (Camargo et al. 2018). Therefore, if the
956 control of this species continues to rely on the use of a single

957 Cry toxin, strict adherence to the HDR strategy is of utmost
958 importance so that the pest does not develop resistance. In
959 the case of the much more widely distributed *O. nubilalis*, no
960 significant decrease in susceptibility to Cry1Ab nor Cry1F
961 has been observed in the USA since 1996 (Tabashnik and
962 Carrière 2019); however, one case of practical resistance to
963 Cry1F-expressing Bt maize (event TC1507) has been docu-
964 mented in a minor maize-growing region in Canada (Smith
965 et al. 2019). Concern about the possible development of
966 resistance to the Cry toxins expressed by Bt maize, together
967 with the social rejection of GM crops in many European
968 countries, make maize breeding for increasing natural resist-
969 ance to maize borers an important complementary approach
970 in pest management, since it would render additional genes
971 to stack in Bt hybrids to slow down the appearance of insect
972 resistance, and improve cultivars for organic and low-input
973 farming (Mohan et al. 2008).

974 RNAi

975 RNA interference (RNAi) refers to an evolutionary con-
976 served mechanism of eukaryotic cells in which dou-
977 ble-stranded RNA (dsRNAs) molecules are involved in
978 sequence-specific suppression of gene expression. Exoge-
979 nously applied or endogenously expressed double-stranded
980 RNAs, complementary to developmentally important genes,
981 trigger a gene-specific cellular mRNA degradation cascade
982 that results in the knock-down of a specific gene (Kourti
983 et al. 2017; Kontogiannatos et al. 2021). The realization that
984 in vitro or in vivo synthesized specific dsRNAs have impor-
985 tant insecticidal properties when applied to insects through
986 spraying or genetic engineering techniques has attracted
987 great interest for research in this field (Kourti et al. 2017;
988 Kontogiannatos et al. 2021).

989 RNAi has already found applications in the pest control
990 industry. For example, Monsanto (now Bayer CropSci-
991 ence) has developed the use of RNAi through a technology
992 called “BioDirect,” in which dsRNAs are applied exoge-
993 nously to protect plants against insects (<https://monsanto.com/innovations/agricultural-biologicals/>) (Cagliari et al. 2019). “SmartStax Pro” maize traits containing both Cry and dsRNA (event DvSnf7) transgenes are expected to be commercialized in 2022 in the USA to control maize rootworms, *Diabrotica* sp. (DiFonzo 2021). Studies have shown that, compared to the Cry Bt maize (e.g., SmartStax), the SmartStax Pro maize containing dsRNAs is effective to control Cry3Bb-resistant rootworms such as the western corn rootworm, *D. virgifera virgifera* LeConte (Head et al. 2017). Additionally, Syngenta scientists are also developing biocontrol products based on RNAi to protect potato plants from attack by Colorado potato beetle (<https://www.youtube.com/embed/BiVZbAy4NHw?ecver=1>) (Cagliari et al. 2019). Despite the aforementioned breakthrough technologies, 1007

1008 RNAi has not been widely used in pest control applications
 1009 because of important technical limitations that must be
 1010 taken into consideration. RNAi efficiency seems to be vari-
 1011 able among lepidopteran species (Terenius et al. 2011) and
 1012 other insect orders as well (Singh et al. 2017). The factors
 1013 that play major roles in this varying effects are seemingly
 1014 the degradation of dsRNA by dsRNases and the presence
 1015 or absence of key RNAi components in the corresponding
 1016 insect cells (Swevers et al. 2013; Singh et al. 2017). Another
 1017 factor that must be taken into consideration with respect to
 1018 RNAi efficiency is the cellular uptake of dsRNA. Previous
 1019 studies showed differential dsRNA transport and uptake pat-
 1020 terns between lepidopteran and coleopteran cell lines and
 1021 tissues but the process of cleaving long dsRNAs into small
 1022 interfering siRNAs could only be achieved by the Coleop-
 1023 teran ones (Shukla et al. 2016).

1024 One of the first reports of successful RNAi in *O. nubilalis*
 1025 was that of Khajuria et al. (2010) (Table 2). In this study,
 1026 researchers were able to silence a chitinase encoding gene
 1027 (*OnCht*) using a feeding-based RNAi technique. Feeding-
 1028 mediated RNAi caused a 64% reduction of *OnCht* in the lar-
 1029 val midgut, an increased chitin content of 26% and decreased
 1030 larval body weight of 54%; however, no insecticidal activity
 1031 was reported (Khajuria et al. 2010). Following the obser-
 1032 vations mentioned above, researchers indicated low RNAi
 1033 efficiency in *O. nubilalis* with both dsRNA injection and
 1034 feeding (Cooper et al. 2020a, b). By comparing the dsRNA
 1035 stability in *O. nubilalis* larval guts and hemolymph with
 1036 that of *D. virgifera virgifera*, a coleopteran exhibiting high
 1037 RNAi efficiency, researchers showed rapid dsRNA degra-
 1038 dation in the European corn borer (Cooper et al. 2020a, b)
 1039 which later was attributed to nuclease activity (Cooper et al.
 1040 2020a, b). The authors further identified complementary
 1041 DNAs putatively encoding four dsRNases (*OndsRNase 1*,
 1042 *2*, *3*, and *4*) and one REase (*OnREase*) (Cooper et al. 2020a,
 1043 b). *OndsRNase2* and *OnREase* were highly expressed in the
 1044 *O. nubilalis* larval gut, and *OndsRNase1* showed the high-
 1045 est expression in hemolymph, especially in older devel-
 1046 opmental stages (Cooper et al. 2020a, b). Transcript level
 1047 analysis after dsRNA exposure revealed that expression of
 1048 *OnREase* rapidly increased upon dsRNA ingestion or injec-
 1049 tion, whereas *OndsRNase4* expression only increased after

1050 long-term ingestion of dsRNA (Cooper et al. 2020a, b). The
 1051 core RNAi pathway genes, Argonaut 2 (*OnAgo2*), Dicer 2
 1052 (*OnDcr2*), and the dsRNA binding protein R2D2 (*OnR2D2*)
 1053 were cloned and characterized in *O. nubilalis* (Cooper et al.
 1054 2021a, b). However, a comparison of evolutionary distances
 1055 revealed potentially important variations in the first RNase
 1056 III domain of *OnDcr2*, the double-stranded RNA binding
 1057 domains of *OnR2D2*, and both the PAZ and PIWI domains
 1058 of *OnAgo2*. Moreover, the introduction of non-target dsRNA
 1059 into *O. nubilalis* second-instar larvae via microinjection did
 1060 not affect *OnAgo2*, *OnDcr2*, or *OnR2D2* expression (Cooper
 1061 et al. 2021a, b). In contrast, ingestion of the same dsRNAs
 1062 resulted in upregulation of *OnDcr2* but downregulation of
 1063 *OnR2D2* (Cooper et al. 2021a, b).

1064 RNAi can be improved by identifying methodologies
 1065 that overcome the biochemical, molecular, and physical
 1066 boundaries imposed by insect cells (Kontogiannatos et al.
 1067 2021). There are many technologies that are currently being
 1068 developed in order to enhance RNAi efficiency, encapsulate
 1069 dsRNAs, and increase cellular uptake (Kontogiannatos et al.
 1070 2021). Of these, more important seem to be the nanoparticle,
 1071 ribonucleoprotein and virus-like particle (VLP)-mediated
 1072 dsRNA encapsulation and delivery (Kontogiannatos et al.
 1073 2021). *Ostrinia nubilalis* ex vivo incubation experiments
 1074 revealed that Meta dsRNA lipoplexes, EDTA, chitosan-
 1075 based dsRNA nanoparticles, and Zn²⁺ enhanced dsRNA sta-
 1076 bility in their hemolymph and gut content extracts, compared
 1077 to the uncoated dsRNA (Cooper et al. 2021a, b). Despite
 1078 that, these formulations failed to enhance RNAi efficiency
 1079 in *O. nubilalis* in vivo (Cooper et al. 2021a, b), meaning that
 1080 other factors must be explored in order to improve RNAi in
 1081 this insect.

1082 Silencing of a juvenile hormone esterase-related gene
 1083 (*SnJHER*) in *S. nonagrioides* using different methodolo-
 1084 gies and dsRNA lengths resulted to a wide range of results
 1085 (Kontogiannatos et al. 2013). For hemolymph larval injec-
 1086 tion, different sizes of the target gene caused efficient gene
 1087 downregulation, but only the longer one which corresponded
 1088 to almost the entire *SnJHER* cDNA resulted in a lethal phe-
 1089 notype (Kontogiannatos et al. 2013). In contrast, admin-
 1090 istration of the dsRNAs at the pre-pupal stage resulted in
 1091 lethal phenotypes regardless of the length of the dsRNA

Table 2 Summary of RNAi experiments performed with *O. nubilalis* and *S. nonagrioides*

Species	Gene	Function	Delivery	Silencing	Phenotype	References
<i>Ostrinia nubilalis</i>	<i>OnCht</i>	Chitin synthase	Feeding	Yes	Chitin content/body weight	Khajuria et al. (2010)
	<i>OnLgl</i>	Lethal giant larvae protein	Injection/feeding	Various	No	Cooper et al. (2021a, b) ^b
<i>Sesamia nonagrioides</i>	<i>SnJHER</i>	Juvenile hormone esterase-related	Injection/feeding/bacterial feeding/baculovirus-mediated	Various	Various	Kontogiannatos et al. (2013)

(Kontogiannatos et al. 2013). The same authors showed that bacterial administration of the dsJHER had no developmental consequence in *S. nonagrioides* larvae, despite the silencing of the gene (Kontogiannatos et al. 2013).

Baculovirus-mediated RNAi in lepidoptera was first described by Hajós et al., (1999). The authors used a recombinant *Autographa californica* multicapsid nucleopolyhedrovirus (AcMNPV) expressing a juvenile hormone esterase (JHE) gene from *H. virescens* in the antisense orientation, driven by a viral p10 promoter (Hajos et al. 1999). The same authors showed that infection with this recombinant virus greatly reduced the hemolymph JHE level and resulted in aberrant morphogenesis of final-instar *H. virescens* larvae (Hajos et al. 1999). A similar approach had been used by Kontogiannatos et al. (2013) in which a recombinant *Bombyx mori* nucleopolyhedrovirus (BmNPV) expressing a hairpin dsRNA of *SnJHER* was used to infect *S. nonagrioides* (Kontogiannatos et al. 2013). The phenotype produced by infection with the BmNPV/dsJHER virus was similar to this of the hemolymph administration of the in vitro synthesized dsJHER but was almost inconclusive for studying RNAi in pupal and adult stages due to its high nonspecific effects at these stages (Kontogiannatos et al. 2013). A medium to a low degree of silencing was observed to the BmNPV/dsJHER infected insects (Kontogiannatos et al. 2013).

RNAi technology is one of the most recent trends in crop protection and it conceptually approaches the “ideal” of the perfect pesticide in that it targets only the intended pest and is expected to have little impact on non-target organisms (pollinators, parasitoids, predators, and vertebrates) (Kourti et al. 2017). Furthermore, it is biodegradable posing little risk to human health and the environment (Kourti et al. 2017). For the reasons stated above, the application of this technology to combat lepidopteran pests, specifically *O. nubilalis* and *S. nonagrioides* requires considerable improvement. Based on our inferences, we believe that new approaches are required for RNAi to be used in the management of lepidopteran pest populations. Technologies involving RNAi that have been shown to be effective in modern medicine (e.g., VLPs, Ribonucleoproteins, etc.) must be investigated for use in RNAi-mediated pest control. These technologies are estimated as able to overcome all obstacles that insect cells pose to RNAi and the future for mass production of RNAi pesticides lies ahead.

Chemical control

Chemical control remains one of the most widely used methods for lepidopteran pest management, particularly in areas where *Bt* maize cultivation is not permitted or has not yet been adopted by farmers. Chemical insecticides are often not effective against *O. nubilalis* and *S. nonagrioides*

infestations due to the prolonged duration of adult flight, the irregular arrangement of egg laying in the field, and especially the rapid penetration of larvae into the plant and cryptic behavior, where they are protected inside against insecticide application (Blandino et al. 2006). An aggravating circumstance is the height of the crop, which often requires the use of specialized machinery including aerial spraying in large cultivated areas.

Chemical control of both species is especially challenging because there is only a narrow window for insecticide application between egg hatch and larvae entering into plants (Shelton et al. 2002). The efficacy of various insecticides used for this purpose is determined not only by the active ingredient and the rate of application, but also by the application conditions, and most importantly, the application timing.

Historically, chemical control of maize borers was done using organochlorides, organophosphates, and carbamates insecticides in their granular form. From the mid-1970s and during the 1980s, synthetic pyrethroids gained importance due to their efficiency and low mammalian toxicity. However, the overreliance on one mode of action increases the likelihood of resistance evolution. Although pyrethroid resistance in *O. nubilalis* has not yet been documented in the USA, lambda-cyhalothrin resistance has been reported in France (Siegwart et al. 2012). Later on, other active ingredients from new insecticide classes were added to the chemical control strategies against maize borers, including biological insecticides. Currently, many insecticides are approved for control of these pests, including: chlorpyrifos-methyl, chlorpyrifos-ethyl, deltamethrin, cyfluthrin, esfenvalerate, lambda-cyhalothrin, cypermethrin, indoxacarb, novaluron, lufenuron, imidacloprid, spinosad, and azadirachtin. These active ingredients include diamides, oxadiazines, benzoylureas, pyrethroids, and a bioinsecticide with different mechanisms of action, reducing the likelihood of insecticide resistance especially if used in rotation (Blandino et al. 2006, 2010; Saladini et al. 2008).

Foliar broad-spectrum insecticides are conventionally applied to maize in many European countries (e.g., Spain, Hungary, Poland, Germany, Italy, and France) to control maize borers and other lepidopteran species. Many fields and laboratory studies have been carried out with the general objective of testing and validating innovative IPM solutions including the sustainable use of pesticides and choosing selective insecticides. Over two years, Ostojčić et al. (2001) tested the efficacy of several insecticides including organophosphates (fenthion, dimethoate, and thiomethone), pyrethroids (cypermethrin and lambda-cyhalothrin) and two *Bt* preparations to control *O. nubilalis* larvae. Organophosphates provided 42 and 32% control in the first and second years of testing and pyrethroids were 40 and 30% effective,

1195 both being similar to the Bt-based preparations (42 and 29%
1196 in the first and the second years of testing).

1197 The insect growth regulators (IGRs) lufenuron, tef-
1198 lubenzuron, and hexaflumuron were investigated over the
1199 course of 3 years with poor to acceptable results in control-
1200 ling *O. nubilalis*, similar to the neonicotinoid imidacloprid
1201 (Bažok et al. 2009). The same study reported that spinosad-
1202 based insecticide showed satisfactory efficacy, while *Bt* var.
1203 *kurstaki* insecticide applications as well as pyrethroids and
1204 organophosphate, alone or in combinations, performed very
1205 well.

1206 New active ingredients representing several chemical
1207 groups such as diamides, oxadiazines, and benzoylureas have
1208 been tested and registered for chemical control of maize bor-
1209 ers. The use of indoxacarb (oxidiazines), chlorantranilprole
1210 and cyantranilprole (diamides) against *O. nubilalis* in the
1211 field gave generally satisfactory results especially in compar-
1212 ison with the active ingredients that have been in use for
1213 decades, although the number of studies is still limited. In
1214 previous investigations, indoxacarb was more effective than
1215 chlorpyrifos but similar in efficacy to alpha-cypermethrin
1216 (Saladini et al. 2008).

1217 Using 2-year data from a long-term experiment in Italy,
1218 Vasileiadis et al. (2017) evaluated the effect of three dif-
1219 ferent foliar insecticide treatments in maize. Lambda-
1220 cyhalothrin (19.5 g a.i./ha), chlorantranilprole (30 g a.i./
1221 ha), and a biological insecticide containing *Bt* var. *kurstaki*
1222 (1000 g/ha) were applied against second-generation lar-
1223 vae of *O. nubilalis*. Results showed greater efficacy of the
1224 broad-spectrum lambda-cyhalothrin and chlorantranilprole
1225 insecticides compared to the Bt-based biopesticide. Superior
1226 efficacy in controlling *O. nubilalis* damage in snap beans
1227 was observed with cyantranilprole compared to bifenthrin
1228 (pyrethroid) (Huseth et al. 2015), and it has been shown
1229 that the anthranilic diamides, especially chlorantranilprole,
1230 exhibit longer-term efficacy than pyrethroids (Schmidt-Jef-
1231 fries and Nault 2017).

1232 Musser and Shelton (2005) investigated the toxicity of
1233 pyrethroids (lambda-cyhalothrin and bifenthrin), carbamate
1234 (methomyl), and spinosyn (spinosad), on maize-borer con-
1235 trol at various temperatures and concluded that increasing
1236 temperatures from 24 to 35 °C reduced pyrethroids' toxicity
1237 of by 9.5–13.6-fold, and spinosad toxicity by 3.8-fold, while
1238 elevated temperatures had no effect on methomyl toxicity. In
1239 order to test the effectiveness of insecticides depending on
1240 the time of application, Blandino et al. (2010) and Saladini
1241 et al. (2008) conducted long-term field trials with different
1242 times of pyrethroid application and found that treatments
1243 performed a week before and during the peak of *O. nubilalis*
1244 adult flight had the highest efficiency. In their 3-year inves-
1245 tigation, Bažok et al. (2009) demonstrated that insecticide
1246 efficacy against *O. nubilalis* was time dependent, with IGRs
1247 and *Bt* insecticides requiring application closer to egg hatch,

1248 and that one insecticide application at the proper (early) tim-
1249 ing resulted in the same efficacy as two successive applica-
1250 tions of the same insecticides.

Roadmap for future research

1251 Since the successful introduction of *Bt* technologies to con-
1252 trol maize borers, research on biology and management of
1253 such pests has been overlooked. However, following reports
1254 of Cry1F resistance in some *O. nubilalis* populations in Can-
1255 ada, there is a renewed interest in studying the phenology
1256 and management of these pests in order to mitigate and man-
1257 age resistant populations. The risk of resistant populations
1258 emerging is high in other parts of the world such as Spain
1259 and Portugal where the majority of *Bt* maize in Europe is
1260 grown especially since only maize expressing the Cry1Ab
1261 toxin is currently authorized for cultivation, and varieties
1262 expressing other Cry toxins are not expected to be allowed
1263 by the European Union in the near future. Furthermore,
1264 pressure from organic consumer grocery markets is causing
1265 subtle shifts toward non-GMO organic dairy feed production
1266 in some maize-producing regions. Such changes are raising
1267 concerns about the resurgence of *O. nubilalis* and other stem
1268 borers. In such cases, it is critical to update the knowledge
1269 and bridge gaps on aspects of maize borer biology in general
1270 as well as these with resistance development.

1271 The resistance discovery in Canada also emphasizes
1272 the critical importance of continuing resistance monitor-
1273 ing efforts for *O. nubilalis* and *Bt* maize as well as research
1274 into cross-resistance among Bt proteins, susceptibility to
1275 all existing Bt proteins, and any new proteins that may be
1276 introduced in the future. Furthermore, resistance monitor-
1277 ing should be extended to alternate host crops for maize
1278 borers' management within their distribution range. Finally,
1279 research on maize natural resistance to stem borers is and
1280 will continue to be necessary because introgression of genes
1281 involved in maize resistance and tolerance would help to
1282 slow the appearance of insect resistance to *Bt* hybrids and
1283 the released varieties would be useful for organic and low-
1284 input farming.

Author contributions

1285 GK and KH conceived and designed the work. GK, AB,
1286 DK, PH, MFGVP, GPF, FH, WDH, BHSS, RAM, AK,
1287 RRR, JLS, ASK, MRPA, and KH provided text based on
1288 bibliography review. All authors revised and approved the
1289 manuscript.

1290 **Supplementary Information** The online version contains supplemen-
1291 tary material available at <https://doi.org/10.1007/s10340-023-01595-8>.

1294 **Funding** Not applicable.

1295 **Data availability** Not applicable.

1296 **Code availability** Not applicable.

1297 **Declarations**

1298 **Conflict of interest** The authors have no relevant financial or non-fi-
1299 nancial interests to disclose.

1300 **Ethical approval** This article does not contain any studies with human
1301 participants or animals (other than insects) performed by any of the
1302 authors.

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