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Review

Alternative Strategies for Controlling Wireworms in Field Crops: A Review

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Abstract: Wireworms, the soil-dwelling larvae of click beetles (Coleoptera: Elateridae), comprise major pests of several crops worldwide, including maize and potatoes. The current trend towards the reduction in pesticides use has resulted in strong demand for alternative methods to control wireworm populations. This review provides a state-of-the-art of current theory and practice in order to develop new agroecological strategies. The first step should be to conduct a risk assessment based on the production context (e.g., crop, climate, soil characteristics, and landscape) and on adult and/or larval population monitoring. When damage risk appears significant, prophylactic practices can be applied to reduce wireworm abundance (e.g., low risk rotations, tilling, and irrigation). Additionally, curative methods based on natural enemies and on naturally derived insecticides are, respectively, under development or in practice in some countries. Alternatively, practices may target a reduction in crop damage instead of pest abundance through the adoption of selected cultural practices (e.g., resistant varieties, planting and harvesting time) or through the manipulation of wireworm behavior (e.g., companion plants). Practices can be combined in a global Integrated Pest Management (IPM) framework to provide the desired level of crop protection.

Keywords: click beetle; crop damage; integrated pest management; risk assessment; pest monitoring; biocontrol; landscape feature; habitat manipulation; companion plant; mutual fund



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1. Introduction

Agriculture is facing major challenges, i.e., global change and societal pressure to preserve the environment. Climate change may progressively alter the spatial distribution of species or their life cycle (e.g., voltinism), raising new concerns about crop protection against pests and pathogens. Societal awareness of the deleterious effects of chemical pesticides and fertilizers for both environmental and human health has increased with the publication and dissemination of studies reporting dramatic declines in animal populations and biodiversity (regarding entomofauna, see for example [1–3]), with change being called for in the agricultural production system, notably toward more environmentally friendly crop-management practices. Such a demand sometimes spreads in the government bodies. In this respect, the European Union introduced Directive 128/2009/EC, which made the implementation of Integrated Pest Management (IPM) principles compulsory, as described by the European network ENDURE (www.endure-network.eu, accessed on 9th of May 2021), and progressively banned various chemical products for which undesirable effects had been evidenced (e.g., neonicotinoids for their severe impact on pollinators [4,5]). New threats to crops concomitantly with a reduced availability of pesticides have put farmers in a difficult situation, and calls have come for alternative strategies to control pests and diseases, both preventative and curative.

The control of wireworms, the soil-dwelling larvae of click beetles (Coleoptera: Elateridae), is a remarkable illustration of this issue, and is the focus of this review. Wireworms, of which there are thousands of species but only a few harmful to agricultural crops, have been notorious as major pests worldwide for a long time. At the beginning of the 20th century, when chemicals were much less used, wireworms were considered the most harmful pests to arable crops [6]. Indeed, they can inflict severe economic damage on several major arable crops (e.g., potato, maize, and cereals) across Europe and North America [7], and the research effort into controlling these pests has risen considerably over the last few decades (Figure 1). Wireworms are extremely polyphagous pests and feed on nearly all cultivated (all cereals; all kinds of vegetables including onions, leek, and garlic; maize; potatoes; sweet potatoes; ornamentals, sugar beet and more) and wild plant species, including weeds. Additionally, most species relevant to agriculture are not only herbivorous but feed also on animal preys available in the soil (insect larvae and pupae or earthworms). Some crops are less susceptible to wireworm damage in terms of stand and yields because of agronomic characteristics (plant growth rate and density, tissues susceptibility, sowing date). This leads to the perception that some crops are specifically attacked while this is in general not the case. Elaterids exhibit a prolonged larval stage in the soil before pupation. Based on their life cycle, they fall into two groups: species overwintering as adults, and species not overwintering as adults [8]. The life cycle lasts 1–5 years [6,9–12], with only the adult stage dwelling outside the soil: a few days for species non-overwintering at the adult stage, and several months for species overwintering at the adult stage. Incidentally, the spatial distribution of species is changing probably due to climate change (e.g., *A. sordidus* is becoming a major pest in parts of Germany [13]). Meanwhile, moratoriums imposed by many countries on neonicotinoid seed treatments, as well as restrictions and deregistration of several active substances, have fostered the search for alternative environmentally friendly solutions for wireworm pest control.

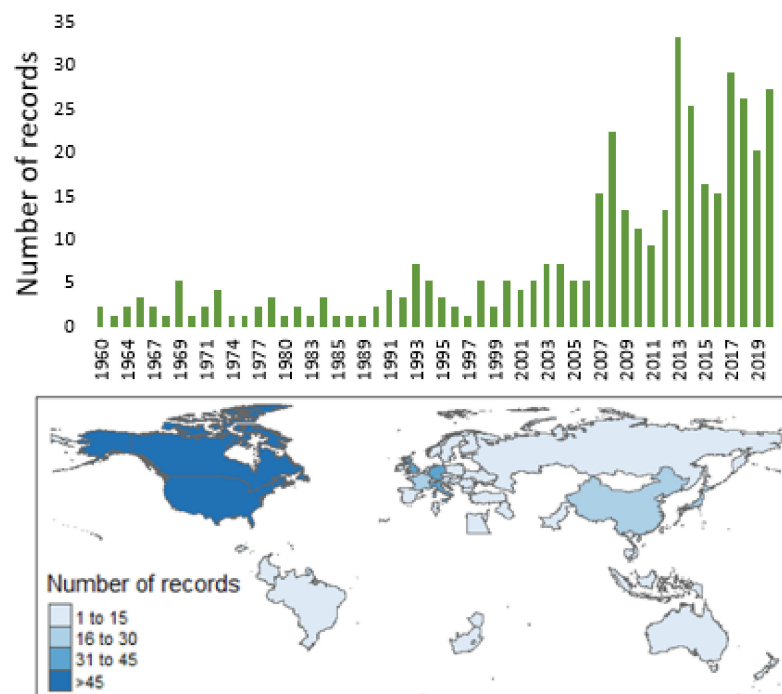


Figure 1. Number of articles published annually from 1960 to 2020 (barplot) and their distribution across countries (world map), according to the Web of Science request formulated on 30 March 2021 as follows: (wireworm* OR (click AND beetle*) OR agriotes) AND (IPM OR biocontrol OR control OR management OR regulation OR “risk assessment” OR “decision support” OR DSS). A total of 386 articles were published over the period under study, with a sharp rise around 2005.

Damage inflicted on crops results from the interaction between wireworm field abundance and host susceptibility under abiotic constraints. Alternative crop-protection strategies to the systematic use of chemicals should target one or both of these two components in order to contain damage under the economic threshold. Achieving this requires an in-depth understanding of pest biology and ecology and of host plant phenology, as well as of the main processes at stake in their interactions. While the sensitive phenological stages of the host crop are often well-known, knowledge of the biology and ecology of wireworms is still incomplete. As an example, while the duration of the feeding phase varies according to larval instar [9,10,14], the entire life cycle of some species still needs to be described (e.g., *A. lineatus*, *A. sputator*).

Strategies aiming at reducing wireworm densities below the economic threshold (when available) should integrate more than one practice with a partial impact and can be achieved through long-term management along the crop rotation and at different spatial scales. Preventive practices include applying crop rotations unfavorable to oviposition and wireworm survival, tilling when edaphic conditions are conducive to destroying soil-dwelling life stages, incorporating plants or extracts with biofumigant and allelochemical properties into soil, the use of natural enemies for pest control, and the manipulation in space and time of favorable areas (e.g., managing grassland regimes). Practices targeting the containment of crop damage below an economic threshold (limitation of harmfulness) despite substantial larval densities rely on identifying optimal planting and harvest conditions, protecting the sensitive crop with attractive companion plants, increasing seeding rates, and planting more tolerant cultivars. Reaching a satisfactory level of crop protection requires a combination of agronomic practices, thereby designing an Integrated Pest Management strategy (IPM) whose foundations are stated in Barzman et al. [15]. IPM faces the challenge of assessing which protection methods are compatible and how to set their combination so that the resulting crop protection has sufficient efficacy.

Our aim in this paper is to provide a comprehensive state-of-the-art of alternative wireworm management practices to insecticide use and suggest a holistic approach to exploiting them as IPM packages that include two or more alternative practices as replacements for insecticides. First, considering that any relevant management strategy requires accurate risk assessment, we address the question of risk assessment in terms of wireworm infestation or crop damage and of wireworm population monitoring. Indeed, a basic efficient alternative to the preventive use of insecticides can be doing nothing when risk is low or waiving the planting of a susceptible crop where and when the risk is high. Then, we present the main pesticide-free methods for controlling wireworms and elaborate on their putative combinations within an IPM framework. Finally, we outline a future research avenue that will lead to reduced use of insecticides for controlling wireworms in field crops.

2. Risk Assessment

Assessing the risk of wireworm infestation or crop damage is the first and most efficient alternative to the preventive use of insecticides, as it provides guidance on the selection of fields with low risk of economic damage. Risk assessment relies on the evaluation of factors that favor field infestation or crop damage and is a preventive tool. In its most advanced form, it consists of a decision-support system. It can also stem from the monitoring of pest populations, at different development stages, mainly at plot scale, and trigger the adoption of corrective tactics or the adaptation of preventive strategies.

2.1. Evaluation of Risk Factors

2.1.1. Risk Factors

Farmers' expertise, studies and reviews dealing with wireworm biology and ecology, and control methods highlight different categories of the factors that drive wireworm infestation and result in crop damage (Table 1).

The feeding behavior of wireworms generally involves periods of inactivity in deep soil layers, mainly in summer or winter when soil environmental conditions are adverse. This inactivity alternates with foraging periods in autumn and spring when soil conditions become more favorable in the upper soil layers [9–11,16–18]. Climate, soil properties, and their interactions influence the vertical migration dynamics of wireworms, thereby influencing the damage they might cause to field crops.

As stated in the introduction, the multiannual biological life cycle of most wireworm species [9–11,19,20] features a prolonged period spent as larvae in the soil before pupation. It outlines the prominent influence of soil characteristics on wireworm infestation and damage. Jung et al. [21] showed preferred ranges of soil moisture by wireworms in relation to four soil types and for different *Agriotes* species. Lefko et al. [22] outline the importance of soil moisture in wireworm survival and spatial distribution, suggesting that soil moisture could reveal areas where wireworms are more likely to occur and could direct scouting within a field. Furlan et al. [23] conducted a long-term survey on maize fields (1986–2014), concluding that organic-matter content was the strongest risk factor for economic damage. The risk of damage increased considerably when its value was greater than 5%. Kozina et al. [24] reported that humus content (%), together with the current crop being grown, was the best predictor of high *Agriotes lineatus* abundance. They also found that soil pH was a strong predictor for the abundance of *A. obscurus* and *A. ustulatus*. Based on a large-scale survey carried out in 336 maize fields over three years in France, Poggi et al. [25] concluded that soil characteristics had a prominent influence on wireworm damage risk, ranking them third after the presence of wireworms and climatic variables, with both pH and organic-matter content also being major factors. The effects of soil texture, drainage, and other factors can be found in the literature (see for example Furlan et al. [23]).

The frequency and intensity of wireworm damage varies across regions. Fields exhibiting high larval populations tend to be spatially clustered [26,27]. The distribution of adult click beetles in the landscape is patchy and can be stable for several consecutive years [28,29]. On a smaller scale, Salt and Hollick [30] confirmed farmers' observation that damage can appear in the same area of the field over several years. Taken together, these features suggest that regional and field characteristics, including agricultural practices and landscape context, are important factors in determining wireworm population (see Parker and Seeney [31]).

It is commonly stated that grasslands, as well as uncropped field margins and areas, provide the most favorable habitat for egg-laying and larval development [10,32], and may act as reservoirs from which larvae and click beetles disperse into adjacent crops [33,34]. Field history, plus landscape context through its effect on click beetle dispersal, may shape the pest abundance at the field scale.

Identifying which wireworm species are present (Figure 2) may be of importance, as wireworm damage is species dependent [35,36]. Several *Agriotes* species are the major contributors to wireworm damage in Europe, but species composition and co-occurrence with other wireworms vary, and other genera, such as *Selatosomus*, *Hemicrepidius*, and *Athous*, can also be very important locally [23,37–42]. In North America, several further genera, including *Selatosomus* (spp. formerly added to *Ctenicera*), *Limonius*, *Conoderus*, *Melanotus*, and *Aeolus*, are also economically important, as are native and introduced *Agriotes* [43–47]. In East Asia, *Melanotus* appear to be important, but there are also damaging species from other genera, e.g., *Agriotes* [48,49]. In a long-term study conducted in north-east Italy, Furlan [35] showed that damage symptoms, and thus crop damage, differed according to species. About the same damage level was observed for one larva of *Agriotes brevis* per trap, as for two larvae of *A. sordidus* or five larvae of *A. ustulatus* per trap. Feeding activity may vary significantly between species, thus calling for management strategies that should be tailored to their seasonal dynamics [50]. Similarly, click beetle species differ in their preferences for soil properties and climate characteristics [51]. When studying the effect of factors on risk damage, researchers may fail to spot an effect when priori species have not been identified. Saussure et al. [52] justified their failure to identify an effect of

soil properties by the fact that they did not distinguish between the wireworm species present in the surveyed fields.

Eventually, agricultural practices alter the pest population and crop damage, thereby providing the components of putative prevention strategies (§3). For example, when appropriately applied, tillage reduces populations of eggs and young larvae by damaging them mechanically. Furthermore, delaying the sowing date may help reduce damage by desynchronizing the period of wireworm presence in the upper soil layers and the period during which the field crop is sensitive to wireworm attacks.

Table 1. List of risk factors driving wireworm infestation and resulting in crop damage. Cited references provide examples of studies evaluating the risk factor, without any claim for exhaustiveness. A considerable effort would be required to achieve an overview of all situations in terms of species × crop × location.

| Risk Factor | Potential for Increasing Damage Risk | Factor Effect | Reference |
|--------------------------------|--------------------------------------|--|------------------|
| Climate | | | |
| Soil temperature | Medium–High | ↑ T °C before seeding ⇒ ↓ damage risk and ~12 °C threshold (<i>Agriotes</i> spp. in maize) ↑ T °C ⇒ ↑ total abundance of wireworm community in cereals, Northern USA ↑ T °C ⇒ ↓ abundance of <i>S. pruininus</i> in cereals | [21,22,24,25,53] |
| Rainfall | Medium | Depends on the species and the period under consideration | [22–25] |
| Soil properties | | | |
| Organic matter content | Medium–High | ↑ OM ⇒ ↑ risk High risk when OM > 5% (<i>Agriotes</i> spp.) | [23–25,52] |
| Soil moisture | Medium–High | ↑ mean frequency of days above a moisture threshold ⇒ ↓ wireworm occurrence (IA, USA) Soil-dependent | [21,22] |
| pH | Medium | Low pH ⇒ ↑ damage risk in maize (<i>Agriotes</i> spp.) Increased abundance in <i>L. californicus</i> with higher soil pH | [24,25,53] |
| Texture | Low | Loam soil ⇒ ↓ damage risk | [22–25,52,53] |
| Drainage | Medium | Bad drainage ⇒ ↓ damage risk | [23,25] |
| Current agricultural practices | | | |
| Sowing date | Medium | Late sowing (maize) ⇒ ↑ risk | [23,25,52] |
| Tillage | Medium–High | Ploughing during summer ⇒ ↓ damage risk in sweet potato | [54] |
| Fertilizer application | Low | Slight decrease in damage caused by <i>Agriotes</i> spp. in maize if fertilization compared to none | [25] |
| Past agricultural practices | | | |
| Tillage | Medium–High | Intense tillage decreases damage risk compared to reduced tillage | [55] |
| Field configuration | | | |
| Topography | Low | No significant effect | [25,32] |
| Exposition | Low | Very weak difference in damage caused by <i>Agriotes</i> spp. in maize | [25,32] |

Table 1. Cont.

| Risk Factor | Potential for Increasing Damage Risk | Factor Effect | Reference |
|--|--------------------------------------|--|---------------|
| Field history | | | |
| Historic of meadows | High | Long-lasting meadow favorable to wireworm damage in maize (community of <i>Agriotes</i> species) | [23,25,52] |
| Crop rotation type | High | Rotation including meadows and second crops ⇒ ↑damage risk in maize (<i>Agriotes</i> spp.) | [23,25,52] |
| Landscape context | | | |
| Meadow (or grassy field margins) adjacency | Medium | Presence of adjacent meadow ⇒ ↑ risk | [23,25,52,56] |
| Species occurrence | | | |
| Species identity | High | Level of damage in maize fields in Italy: <i>A. brevis</i> most harmful, then <i>A. sordidus</i> and <i>A. ustulatus</i> Different best predictors in <i>Agriotes</i> wireworm abundance in Croatia. E.g.: <i>A. brevis</i> → previous crop grown; <i>A. sputator</i> → rainfall; <i>A. ustulatus</i> → soil pH and humus Different predictors of wireworm abundance in northern US cereal fields. E.g.: <i>L. infuscatus</i> → crop type and soil texture; <i>L. californicus</i> → crop type, soil moisture, and soil pH | [24,35,53] |

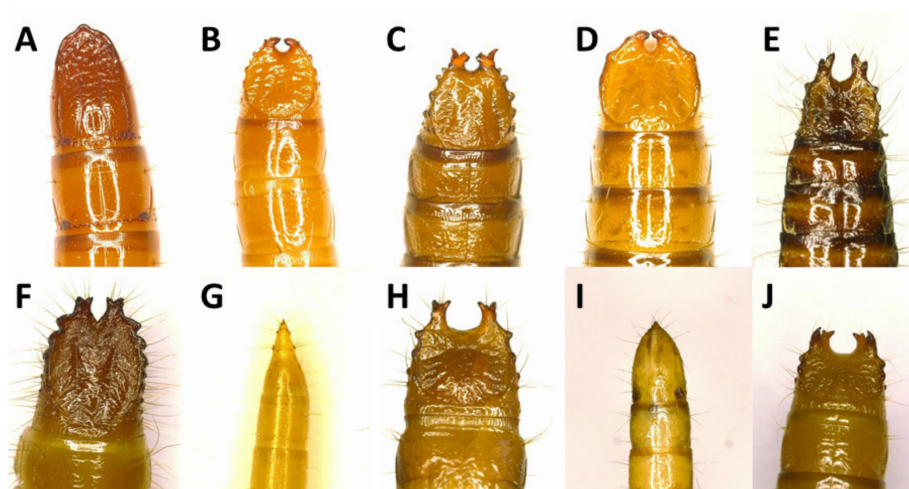


Figure 2. Variability in rear end for wireworm species from different genera. (A) *Melanotus punctolineatus*, (B) *Cidnopus aeruginosus*, (C) *Athous haemorrhoidalis*, (D) *Cidnopus pilosus*, (E) *Prosternon tessellatum*, (F) *Agrypnus murinus*, (G) *Adrastus* sp., (H) *Hemicrepidius niger*, (I) *Agriotes sputator*, and (J) *Selatosomus aeneus*.

2.1.2. Decision-Support Systems

Building on the knowledge of risk factors, a range of models have been able to predict wireworm occurrence based on soil and meteorological data coupled with a hydrologic model [22]; click beetle abundance based on climatic and edaphic factors [24]; wireworm activity based on soil characteristics [21]; their abundance and community structure [53]; correlation between the damage caused in potato fields and landscape structure [56]; and to determine the key climate and agro-environmental factors impacting wireworm damage [23,25,52].

The hypothesis of the vertical distribution of wireworms depending on soil moisture, soil temperature, and soil type was verified by Jung et al. [21], who developed the prognosis model SIMAGRIO-W used as a decision-support system to forecast the (*Agriotes* spp.)

wireworm activity based on edaphic properties. Albeit successfully applied in field tests in western Germany, the model performed poorly when it was evaluated in eastern Austria, and research effort is still needed to improve the current model.

Analyzing long-term survey data from maize fields in northern Italy, in which *Agriotes brevis*, *A. sordidus*, and *A. ustulatus* were identified as the predominant pest species, Furlan et al. [23] calculated risk level based on the different weights of the studied risk factors (defined by relative risk values). A simple decision tree was suggested for practical IPM of wireworms [57,58].

The decision-support system VFF-QC (web application: <https://cerom.qc.ca/vffqc/>, accessed on 9th of May 2021) was originally developed in Quebec (Canada) from a huge database that included more than 800 fields (maize, soybean, cereals, and grasslands), which were characterized by a set of factors (e.g., agricultural practices, soil type, humidity, and organic matter content) and wireworm trapping between 2011 and 2016 [59]. A predictive model based on boosted regression trees assessed the risk level (low, moderate, or high) of finding wireworms in abundance and determined if the field had reached a threshold that would justify treatment. To the best of our knowledge, VFF-QC is the most-used decision-support system for wireworm risk assessment, partly due to rules adopted in 2018 by the Government of Québec that force agronomists to justify the need for seed treatment before prescribing or recommending them to growers.

Using a similar statistical approach, Poggi et al. [25] examined the relative influence of putative key explanatory variables on wireworm damage in maize fields and derived a model for the prediction of the damage risk; they also assessed their model's relevance in providing the cornerstone of a decision support system for the management of damage caused by wireworms in maize crops.

As a whole, these decision-support systems rely on correlative approaches that unravel the potential of a dynamic landscape to shape wireworm populations and eventually crop damages. The development of models that describe the mechanisms driving wireworm colonization, and subsequently elucidate the ecological processes that operate at the landscape scale, remains an avenue for future research.

2.2. Monitoring and Thresholds

2.2.1. Adult Monitoring

Monitoring soil-dwelling pests is difficult and expensive; thus, efforts have been made to assess population levels of click beetles in the hope of inferring larval abundances or crop damage. The identification of click beetle pheromone goes back to the 1970s in the USA for *Limoni* species [60,61] and the 1990s in Europe for *Agriotes* species [62]. Pentanoic acid and hexanoic acid were identified as pheromone compounds for *Limoni* species. Esters of geraniol are the main components of *Agriotes* natural sex pheromones [63], given that female pheromone glands contain up to 24 substances [62]. Varying the mixture formulation allows each species to be caught selectively or, alternatively, several of them to be attracted to the same trap [64]. Recently, several kinds of pheromone traps have been developed and used as research tools to monitor populations in both Europe and North America [24,26,65]. The female sex pheromones of most major European click-beetle pest species (*A. brevis*, *A. lineatus*, *A. obscurus*, *A. proximus*, *A. rufipalpis*, *A. sordidus*, *A. sputator*, *A. ustulatus*, *A. litigiosus*) have been characterized [64]. YATLORF (Yf) sex pheromone traps (Figure 3A) were designed for a range of *Agriotes* species, including all of the most harmful ones in Europe and part of the *Agriotes* pests in North America. In addition, a ground-based pheromone trap for monitoring *Agriotes lineatus* and *A. obscurus* was developed to catch *A. obscurus* and *A. lineatus* in North America [66]. The apparent ease with which pheromones can be used and their potential as a pest management tool have made them attractive for pest monitoring. However, relating click beetles' catches to larval densities requires a good understanding of the pest behavior, pheromone lure reach, and effects of various abiotic factors on trapping [67]. Pheromone traps for *A. lineatus* and *A. obscurus* may have a very short attraction range (below 10 m) [68,69] with no directional bias [70,71].

Significant association was found between male click-beetle catches in pheromone traps and subsequent wireworm abundance and maize damage in the nearby area for three species: *A. brevis*, *A. sordidus*, and *A. ustulatus* [57]. For example, when Yf *A. ustulatus* catches exceeded 1000 beetles per season, there was a 20-fold higher probability that the trapped wireworm density exceeded five larvae per trap. The procedure and thresholds described in Furlan et al. [57] allow both farm-scale and area-wide monitoring, resulting in the drawing of risk maps in cultivated areas and enabling IPM of wireworms to be implemented at a low cost. They make wireworm risk assessment highly reliable, especially when it is associated with agronomic risk factor assessment. In contrast with these results, Benerfer et al. [72] concluded that the proportion and distribution of adult male *A. lineatus*, *A. obscurus*, and *A. sputator* species may give a very misleading picture of the proportion and distribution of wireworm species in the soil, at least when they are caught with sex pheromone traps. However, this study had major constraints, including the fact that fields were observed for one year only while click beetles are associated with wireworm populations in the subsequent years. A longer period of study using more consistent methods might have revealed significant associations between click beetles trapped in previous years and wireworm population levels at year zero. In any case, as noted in a review on their use [73], pheromone traps are sensitive enough to detect low-density populations, and trapping systems are able to inform growers about the presence or absence of wireworm infestation.

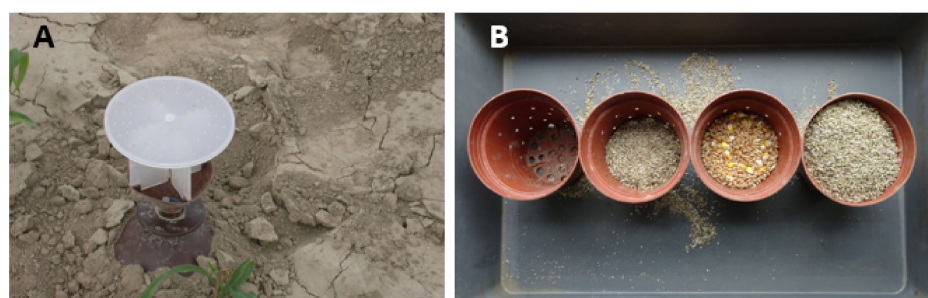


Figure 3. Illustrations of trapping systems. (A) Click-beetle pheromone trap YATLORF. (B) Wireworm bait trap (right pot) and sequential filling of the trap with an empty trap (left pot), a trap with a layer of vermiculite (second pot from left), a trap with a layer of vermiculite and a layer of germinating maize and wheat (second pot from the right).

2.2.2. Larval Monitoring

A considerable amount of work has been done in North America and Europe to assess the potential of replacing time-consuming soil sampling with in-field wireworm bait stations [32]. Due to the sampling effort they require and the non-random distribution of the larvae in fields [30], soil sampling is of little interest [32]. Bait systems utilize the attraction of wireworms by the CO₂ given off by respiring seeds [74]. Wireworms probably perceive CO₂ via clusters of sensilla on the maxillary and labial palps [75]. This probably accounts for the fact that although a large range of vegetable- and cereal-based baits have been tested, baits based on germinating cereal seeds tend to be the most effective [32,76]. In addition, baits based on germinating cereal seeds put in pots (Figure 3B), proved to be an unbiased, time-saving monitoring tool for *Agriotes* wireworms. Since significantly more larvae are found inside the pot than in the other trap types (i.e., plates and mesh-bags), this method can be used without the time-consuming evaluation of the surrounding soil cores [77]. This trap design proved to be effective for attracting non-*Agriotes* species (*Aeolus mellillus*, *Limonius californicus*, *L. infuscatus*) as well [78]. The catch potential of pot baits can be augmented by increasing the number of pot holes [79]. Various techniques for improving the efficacy of wireworm bait systems have been tested. These include covering the bait with plastic [80,81] to raise the soil temperature. The trap designed by Chabert and Blot [80], a modified version of the trap described by Kirfman et al. [81],

comprises a 650 mL plastic pot (10 cm in diameter) with holes (the ordinary number of those used for tree nursery) in the bottom. The pots are filled with vermiculite, 30 mL of wheat seeds, and 30 mL of maize seeds; they are then moistened before being placed into the soil 4–5 cm below the soil surface, after which they are covered with an 18 cm diameter plastic lid placed 1–2 cm above the pot rim. These traps have been used long term following a standardized procedure by Furlan [35]: traps were hand-sorted after 10 days when the average temperature 10 cm beneath the surface was above 8 °C [9,10] to ensure that the bait traps stayed in the soil for an equal period of wireworm activity. The final number of larvae was assessed under the aforementioned conditions, regardless of larvae behavior on individual days. Population levels should be assessed only when humidity is close to field water capacity. Indeed, dry top-soil forces larvae to burrow deep beneath the surface, away from the bait traps [9], and high humidity (flooding in extreme cases) prevents larval activity since all the soil pores are full of water and contain no oxygen.

2.2.3. IPM Thresholds

IPM implementation needs a standardized monitoring method combined with reliable damage thresholds. The aforementioned bait-trap monitoring method has given reliable results over sites and years and might be considered as a standard both for ordinary wireworm IPM implementation and for the assessment of damage thresholds for other wireworm species/crop combinations.

Although increasing literature about wireworms has been published over the last few years (Figure 1), to our knowledge, only four papers report practical IPM damage thresholds, with them being restricted to five species and two crops: *Melanotus communis* thresholds in sugarcane crops [82], *Agriotes brevis*, *A. sordidus*, *A. ustulatus* [35,57], and *A. lineatus* [80] in maize crops. Published thresholds are summarized in Table 2. Other papers supply information about crop susceptibility to wireworms that allows an indirect estimation of damage thresholds. Furlan et al. [20] carried out pot trials that introduced the same number of wireworms per pot for different crops. Results showed a large variation in crop susceptibility. A number (6/pot) of wireworms (*A. ustulatus*, *A. sordidus*) causing a 50% maize and sunflower plant loss, had a negligible effect on soybean but killed most of the sugar-beet seedlings. Likewise, Griffith [83] demonstrated differences in plant susceptibility to wireworm attacks in laboratory tests. Larvae of *Agriotes* spp. were presented with a choice between the seedlings of test plants and of wheat, which is known to be susceptible. Some plants, e.g., onion, were as susceptible as wheat to wireworm attacks, whilst others (mustard, cabbage, French marigold, clover, and flax) were attacked less often. All pea and bean plants exposed to wireworms were attacked, but most tolerated the attacks and continued to grow. Old generic thresholds based on larval density assessed by soil sampling have low scientific reliability and little practical potential [32], one reason being that none of the wireworm species studied were specified.

Table 2. Published damage thresholds according to click-beetle species, crop, and monitoring method.

| Elateridae Species | Crop | Tool | Threshold (Larvae/Trap) | Threshold (Beetles/Season) | Threshold | Reference |
|---------------------------|-----------|--------------------------------------|------------------------------|----------------------------|------------------------------------|-----------|
| <i>Agriotes brevis</i> | Maize | Bait trap | 1 | | | [35,57] |
| <i>Agriotes sordidus</i> | Maize | Bait trap | 2 | | | [35,57] |
| <i>Agriotes ustulatus</i> | Maize | Bait trap | 5 | | | [35,57] |
| <i>Agriotes lineatus</i> | Maize | Bait trap | 1–2 (seeding before 1st May) | | | [80] * |
| <i>Agriotes brevis</i> | Maize | Yf pheromone trap | | 210/450 | | [57] |
| <i>Agriotes sordidus</i> | Maize | Yf pheromone trap | | 1100 | | [57] |
| <i>Agriotes ustulatus</i> | Maize | Yf pheromone trap | | 1000 | | [57] |
| <i>Melanotus communis</i> | Sugarcane | Soil samples taken in sequence to 25 | | | 8 wireworms found in total samples | [82] |

* Derived data published in the cited paper; plant damage was lower than 15% with 1–2 wireworms per trap. Wireworm plant damage lower than 15% in maize should not result in yield reduction [23].

3. Pest Population Management

The current resurgence of wireworm damage to various crops has resulted in a strong demand for new agroecological methods to control those pests, notably consequential to the reduced availability of pesticides, possibly in response to global changes and pressing demands by the general public for the implementation of more environmentally friendly agricultural practices. Accordingly, continuous advances in the knowledge of click-beetle biology and ecology have led to several new management practices currently being tested or developed. New proposals mostly originate from (1) the field of agricultural sciences, with them promoting relevant cultural or mechanical methods (use of resistant/tolerant crops, design of bespoke tilling strategies or rotation); (2) the field of chemical ecology (use of pheromones for sexual confusion); (3) the field of trophic ecology (biological control); and (4) from the field of landscape ecology (large-scale habitat management to reduce pest pressure at landscape scale).

3.1. Cultural or Mechanical Control

3.1.1. Effect of Rotation

The first prevention strategy when controlling wireworm populations is to plan a diversified ecosystem that includes a rich rotation with crops and cover crops placed in the most suitable positions. Crops susceptible to wireworm damage should be placed after crops that do not favor or that reduce wireworm populations (e.g., incorporating barley and oats into crop rotations can reduce wireworm attacks [84]). Crop diversification can benefit wireworm control. For instance, mustard, cabbage, French marigold, clover, and flax are less susceptible to attack, while pea and bean plants tolerate attacks [83]. Hence, large intensively tilled (e.g., hoed) inter-row crops and/or biocidal cover crops directly reduce wireworm populations [85,86]. Generally speaking, cover-crop choice can contribute to wireworm cultural control both through its effect on soil biodiversity and ecosystem stability and through its biofumigant/biocidal effect. Crop choice can contribute to wireworm mechanical control by increasing larval mortality, either due to tillage interventions when preparing sowing beds or to hoeing in large inter-row crops.

3.1.2. Effect of Tilling

As the life cycles of wireworm species last several years and take place largely in soil, tillage may impact several of their life-history traits. During the oviposition period in spring, females lay their eggs in the top soil-layer [10,20] in a steady environment, such as litter or grass, whenever possible, because of their own sensitivity to temperature fluctuations [6] and their eggs' sensitivity to desiccation. After hatching, larvae are exposed to soil tillage, in particular to ploughing, making them vulnerable to predation [55] or desiccation [87]. In 1949, Salt and Hollick [55] conducted a five-year experiment, which highlighted that the decline in wireworms was accompanied by an outstanding change in the distribution of larvae sizes, reflected by a decrease in the number of young larvae. It is currently acknowledged that, due to a lack of soil cover, oviposition might be reduced on row-crop compared with grassland [19,32]. Seal et al. [54] found that ploughing three times during the summer reduced wireworms collected at bait traps from 1.75 per bait trap to 0.2 per bait trap, compared to no change in unploughed control plots. This reduction was attributed to exposure to bird predation and desiccation. Larval mortality depends on tillage timing, which should match the egg-laying and first instar larvae periods, which are the most susceptible to unfavorable soil conditions. The best tillage timing for interfering with wireworm population dynamics varies with the species life-cycle. For example, in Italy, overwintering *A. sordidus* adults emerge from their cells in the soil from late March–early April and start to lay eggs from May onwards [10]; thus, susceptible instars (eggs and young larvae) occur in the soil from May to June, usually peaking in May. Therefore, tillage from mid-May to late June, as preparation of seed beds for the subsequent crop and hoeing in row crops can dramatically reduce subsequent wireworm populations.

3.1.3. Effect of Water Management

The effect of drying and flooding has been studied mainly on the American West Coast [16,88–90] and in British Columbia [91]. Irrigation timing may play a role in interfering with wireworm population dynamics. The drying of the top-most soil layer just after eggs are laid can be an effective means of controlling wireworms. Soil drying could be achieved by withholding irrigation from alfalfa before harvest, but it is nevertheless more effective in lighter sandy soils [88]. The main challenge of water management as a control lever is the different response of species according to soil moisture. While *Ctenicera pruinina* (Horn) has long been a pest of dryland wheat [92] and disappears as a pest when fields are converted to continual irrigation [93], *Limonius californicus* do not survive well in dry soil and prefer soil with 8–16 percent moisture [16,89]. Another challenge is the ability of some species to adapt to soil moisture [94]. Despite damage often being reported in soils that flood in the winter, field flooding can effectively reduce *Agriotes* wireworm populations when combined with high temperatures [91]. Lane and Jones [95] highlighted the relationship between soil moisture and temperature on the mortality of *Limonius californicus* larvae. At 30 °C, all larvae submerged under soil and water were killed in four days, whereas only 26 percent of larvae died after 21 days when temperatures dropped below 10 °C. It was also demonstrated that alternating periods of soil flooding and drying is effective for reducing wireworms [96].

3.2. Semiochemical Control

Since the 1970s, regular progress has been made in elucidating the composition of click-beetle pheromones. Synthetic mixtures are now available for several species of agricultural importance, opening new perspectives for using them in wireworm monitoring or even developing new control strategies that rely on adult sexual confusion or mass-trapping.

Besides their potential use for establishing wireworm populations (see Section 2.2), pheromone traps might be used to reduce populations, either through mating disruption or through mass-trapping. Mass-trapping was successfully implemented in Japan to control *Melanotus okinawensis* on sugarcane, with adult densities being reduced by approximately 90% after six years of mass-trapping with 10 pheromone traps per hectare [97]. By contrast, a similar study observed no reduction in *Melanotus sakishimensis* abundance [98]. For *Agriotes* species, the limited attraction range of pheromone traps exacerbates the challenge of mass-trapping and requires a dense network of traps to be set up if populations are to be reduced. Hicks and Blackshaw [70] estimated that suppressing *Agriotes* populations using mass trapping would be prohibitively expensive (2755 €/ha/year), requiring four years of trapping with 10 traps/ha for *A. obscurus*, 15 traps/ha for *A. obscurus*, and m for *A. sputator*. In a long-term experiment on potatoes, Sufyan et al. [99] captured 12,000 specimens belonging to three *Agriotes* species over a period of five consecutive years without any effect on the subsequent larval densities or on potato damage. In 2014, Vernon et al. [100] indicated that arrays of traps spaced 3 m apart potentially disrupted mating but also showed that only 85.6% of the released *A. obscurus* were recaptured. As pointed out by Ritter and Richter [101], mating disruption may be easier for short-lived adult populations that are protandrous and exhibit a short, well-defined swarming period. Work is still in progress on the use of pheromone traps [102] to estimate wireworm population levels for IPM programs [57,68].

3.3. Biological Control of Wireworms

Inundative releases of natural enemies to control pests have been implemented for many years and may be a way to control wireworms in the future. In Europe, this is successfully performed by mass releases of *Trichogramma* wasps against the European Corn Borer (*Ostrinia nubilalis*) in Germany, a *Metarrhizium* product for the control of June chafer larvae (*Phyllopertha horticola*) in Switzerland, or a *Metarrhizium* granule for control of black vine weevil larvae (*Otiorhynchus sulcatus*) as well as a variety of uses of entomopathogenic nematodes against different horticultural pests. Van Lenteren et al. [103]

describe a wide variety of further uses worldwide. Kleespiess et al. [104] showed there are also some potential candidates for wireworm control. Currently, the main focus is on entomopathogenic fungi, with some research also being done on nematodes and combinations of different organisms.

3.3.1. Wireworm Predators

Numerous vertebrates are predators of elaterid larvae and adults, but birds seem to be the major group with more than 100 different bird species mentioned for Europe and North America [105–107]. Mammals, plus amphibian and reptilian predators, are probably of lower importance than birds [105,106]. However, general predation by vertebrates is unlikely to substantially lower wireworm numbers over a large area, even though attempts to use poultry for this purpose were made early on [106]. Predation of click beetles and wireworms by other arthropods, especially by large predatory beetles (Carabidae, Cicindelidae, Staphylinidae) or predatory flies (Asilidae, Therevidae), has occasionally been observed [106,108–110], but as unspecialized predators, they only remove occasional wireworms or beetles. *Agriotes* larvae are predominately, but not exclusively, herbivorous, while species of other genera are predominantly or fully carnivorous [110–112].

3.3.2. Wireworm Parasitoids and Parasites

Generally, wireworms with infections or parasitoids are not commonly found in the field [104,113]. Studies listed by Subklew [106] found no parasitoid in *Horistonotus uhleri*, *Limonius californicus*, *Sinodactylus cinnamomeus*, and *Selatosomus aeripennis destructor* (formerly *Ctenicera aeripennis destructor*). Kleespiess et al. [104] examined about 4000 *Agriotes* spp. larvae mainly from Germany. Of these wireworms, only 25 were infected by entomopathogenic fungi, 29 by nematodes, and 66 by bacteria.

Entomopathogenic bacteria (EPB) appear to be the least tested group of microorganisms against wireworms, although they have been known for considerable time. Langenbuch [114] mentioned an unknown bacteriosis in wireworms. Recently a new bacterium (*Rickettsiella agriotidis*) was found and described [104,115], but no information has been published about its potential associated mortality. Danismaszoglu et al. [116] found that some members of the bacterial flora of *Agriotes lineatus* and related bacteria caused mortality up to 100%. Mites, in most cases probably from the family Tyroglyphidae, commonly occur on field-collected wireworms (Figure 4A). Whether these mites have a parasitic or phoretic connection to the wireworms is unknown, but the latter appears more likely [105].

3.3.3. Hymenoptera

Few hymenopteran parasitoids of soil-inhabiting wireworms are known. For Europe, Subklew [106] lists records mainly of *Paracodrus apterogynus* (Proctotrupidae), but other *Proctotrupidae* and partly unidentified Hymenoptera also appear. *P. apterogynus* is a gregarious parasitoid with several individuals (Figure 4B), but a low percentage of males, emerging from a single wireworm [117]. Known hosts of *P. apterogynus* are *Agriotes obscurus*, *Agriotes lineatus*, and *Athous* sp. [113,117–120], indicating that different genera and species are attacked. Another species, *Pristocera depressa* (Bethylinidae), is a solitary parasitoid of *Agriotes obscurus* [121] and perhaps further species. Females of *P. apterogynus* and *P. depressa* are wingless, indicating that both species search for their wireworm hosts underground. According to D'Aguilar [113], only five of several thousand *Agriotes* larvae from a site in Brittany (France) were parasitized. The parasitism rate seems to be similarly low in Germany, with only two of several thousand wireworms from all over the country being parasitized by a gregarious hymenopteran, most likely *P. apterogynus* (Lehmhus, unpublished). In a few cases, parasitoid Diptera larvae were also found [106,122]. Due both to the rare occurrence of insect parasitoids in economically relevant wireworms and to specific parasitoid biology, they are unlikely to be suitable for mass rearing and augmentative biocontrol.



Figure 4. Illustrations of wireworm biocontrol agents. (A) Mite infestation of an *Agriotes ustulatus* wireworm; it is unclear if these mites are parasitic or phoretic, but heavy infestations appear to affect wireworms negatively; (B) *Agriotes* sp. wireworm with gregarious hymenopteran parasitoid, most likely *Paracodrus apterogynus*; (C) *Agriotes sordidus* infested by the nematode *S. boemarei* (strain FRA48, Lee et al. 2009) carrying the symbiotic bacterium *Xenorhabdus kozodoii* FR48; and (D) *Agriotes lineatus* wireworm with *Metarrhizium brunneum* infestation. Photographs A, B, D: JKI. Photograph C: INRAE-DGIMI.

3.3.4. Nematodes

Nematodes of the family *Mermithidae* parasitize arthropods, mainly insects with at least 15 different orders as hosts [123]. The use of *Mermithidae* has been discussed for biocontrol of mosquitoes [124], but they are occasionally also found in click beetles or wireworms [122,125]. Considering the low densities and propagation difficulties, they are not considered to be suitable candidates for wireworm control.

Entomopathogenic nematodes (EPN) from the genera *Steinernema* and *Heterorhabditis* (Nematoda: Steinernematidae, Heterorhabditidae) with their bacterial symbionts *Xenorhabdus* spp. and *Photorhabdus* spp. (Gram-negative Enterobacteriaceae) are bacterium–nematode pairs and pathogenic to a broad range of insects (Figure 4C). Species from both nematode genera have also been successfully implemented in biological control of insect pests throughout the world [126]. However, wireworms often show very low susceptibility [127] or are sometimes even considered to be resistant to EPN [128]. This may partly be due to unsuitable species combinations, as there are also several cases with successful infection by EPN and damage reduction in the field [129–131]. For example, larvae of *A. lineatus* were reduced by *Heterorhabditis bacteriophora* and *Steinernema carpocapsae*, but not by *Steinernema feltiae* [132,133]. Lehnhus [42] showed differences in mortality for the same three EPN when they attacked four common European wireworms *Agriotes lineatus*, *A. obscurus*, *A. sputator*, and *Selatosomus aeneus*. All EPN did cause mortality in the three *Agriotes* species, but *S. feltiae* failed to cause mortality in *S. aeneus*, which was also the least sensitive wireworm to the other EPN. According to Campos-Herrera and Gutiérrez [127], a Spanish isolate of *Steinernema feltiae* performed poorly against *Agriotes sordidus*. Ansari et al. [132] demonstrated that there were considerable differences in the mortality of a wireworm (*Agriotes lineatus*) caused by different EPN species and even by different strains of a single EPN species (0–67% mortality). Rahatkah et al. [134] showed that after injection of infectious juveniles, the immune reactions of the same wireworm species (*Agriotes lineatus*) to different nematode species (*Heterorhabditis bacteriophora* and *Steinernema carpocapsae*) differed with a higher encapsulation of infectious juveniles from the former, which may be one reason for nematode strains performing differently. Morton and Garcia del Pino [135]

found that the mortality of *Agriotes obscurus* in the lab was dependent both on nematode species and on infectious juvenile dose rates, while under field conditions, a dose of 100 IJs/cm² and the best performing strain *Steinernema carpocapsae* (Weiser) B14 still resulted in nearly 50% mortality. These results indicate that in entomopathogenic nematodes, the control achieved against wireworms is, besides the environmental factors discussed below, dependent on the concentration of infectious juveniles and on the combination of nematode strain and wireworm species.

3.3.5. Fungi

In the field, fungal pathogens can occasionally influence wireworm or click beetle survival greatly. In Switzerland, *Zoophtora elateridiphaga* was described by Turian [136] as attacking *A. sputator*. According to Keller [137], infection rates of *A. sputator* click beetles in Switzerland with *Zoophtora elateridiphaga* (Entomophthoraceae) varied between 72.6% and 100%. The same fungal pathogen occurred at one location near Braunschweig, Northern Germany, in *A. obscurus* and *A. sputator* click beetles, but with only about 10% becoming infected (Lehmhus personal observation 2013, determination of pathogen R. Kleespiess). Entomophthoraceae are comparatively sensitive, difficult to preserve and propagate, and unsuitable for most spray applications, and thus achieving long-term viability is often quite difficult [138]. However, as Keller [139] observed *Z. elateridiphaga* also attacking adults of *Notostira elongata* (Miridae) and achieving growth of colonies on Sabouraud Dextrose Agar (SDA), the host range of this fungus may be less narrow and cultivation less difficult than generally thought. A remaining problem is that attacks by this fungus are directed at adults.

More promising are the entomopathogenic fungi *Beauveria bassiana* (Cordicipitaceae) and *Metarrhizium anisopliae* sensu lato (Clavicipitaceae), including related forms like *M. brunneum* (Figure 4D). These naturally soil-inhabiting fungi are widely recognized as interesting biological control agents against several insect pests [140] and have been known to kill wireworms for more than 100 years [105]. The mechanisms involved in the infection process in wireworms have already been described in detail (e.g., [141,142]). Trials have been conducted with several different strains of both fungi (*Beauveria bassiana* and *Metarrhizium anisopliae* sensu lato, including *M. brunneum*) at different application rates and with different wireworm species both in the field and in the laboratory. The results were quite variable. A commercial product containing a *Beauveria bassiana* strain reached efficacy values between 54% and 94% against *Agriotes* spp. in the field in Northern Italy [143], but in other regions, no differences between potato plots treated with this product and untreated plots were observed [144,145]. Eckard et al. [146] showed differences in mortality for three different strains of *Metarrhizium brunneum* in the three most common European species: *Agriotes lineatus*, *Agriotes obscurus*, and *Agriotes sputator*. Species and stages of five North American elaterid species differed markedly in resistance to attack by a strain of each of the two entomopathogenic fungi *Metarrhizium anisopliae* and *Beauveria bassiana* [147]. Kabaluk et al. [122] tested 14 isolates of *Metarrhizium anisopliae* against three species of wireworms. The North American *Ctenicera pruinosa* was susceptible to most isolates, while *Agriotes obscurus* was highly susceptible to four isolates, and *Agriotes lineatus* was the least susceptible species. Under these circumstances, it is clear that a suitable combination of wireworm species found in the field and EPF strain used is needed to achieve high control effects. A further constraint may be that some bacterial symbionts of wireworms could actively suppress the infection by entomopathogenic fungi [148], which may explain control failures when environmental conditions and the combination of species and strain seem to fit.

3.3.6. EPN and EPF Use Generally

Both environmental and behavioral factors will further affect the infection of wireworms with entomopathogens (EPN and EPF likewise). The retaining of sufficient moisture is indispensable for the growth of entomopathogenic fungi [149] and has to be solved some-

how for reliable control. According to Kabaluk et al. [122], Rogge et al. [150], and Kabaluk and Ericsson (2007), additional factors such as temperature, exposure time, conidia soil concentration, and food availability also affect mortality rates of wireworms when exposed to *Metarrhizium anisopliae*. However, while lower temperatures slow down the spread of wireworm infection [151], the desiccation commonly experienced under summer conditions might affect the viability of EPF in soil. Additionally, wireworms can perform seasonal movements to forage in favorable conditions and to avoid unfavorable ones [9,32,50,114,152–155], meaning that wireworms may escape a biocontrol agent used when the lethal potential of an entomopathogen is not reached shortly after application. For example, infection late in the potato-growing season would probably not prevent damage to daughter tubers. Therefore, the temperature conditions under which the infection cycle of an isolate has its optimum must be considered. For early season applications, a more northern fungal isolate adapted to lower temperatures [156] might even enable crop protection early in the year for such crops that need to be protected as young plants. A temperature effect on the pathogenicity of EPN is also known [157,158], albeit not documented for pathogenicity against wireworms. A further constraint is that the soil type can also influence the effectiveness of biological wireworm control [159]. This has also been described for other insects, partly with contradicting results of higher EPN efficacy in sandy soil than in clay soil, or vice versa [160–162].

In contrast, the origin of inoculum had no significant effect on the virulence of a *Metarrhizium brunneum* strain. The mortality of wireworms treated with spores from host cadavers was similar to the mortality of wireworms treated with spores from a modified Sabouraud Dextrose Agar (SDA) after ten sub-cultivations [146]. Therefore, in general, virulence should not be affected by the conidia production method.

According to Ericsson et al. [163], the biological insecticide Spinosad interacted synergistically with *Metarrhizium anisopliae* against *Agriotes lineatus* and *A. obscurus*, indicating that combinations with a second stressor (insecticide, EPN, or EPF) might enhance biological control. <the synergistic or additive effects of combined use of EPN, EPF, and EPB have been shown for several other pests [164–167].

Several studies [168–172] show that the application pattern is another important point to consider, with banded or spot application being particularly useful.

Nevertheless, in many cases, results achieved by biological control are not yet satisfactory compared to an effectiveness between 50–90% achieved by plant protection products based on the insecticides carbosulfan, fonofos, findane, fipronil, imidacloprid, thiamethoxam, or bifenthrin used in the past [143,173,174]. However, even an array of insecticides tested on five different wireworm species in three elaterid genera demonstrates that there are clear differences in mechanisms, symptoms, and mortality, with even chemical insecticides failing to remove all wireworms [175].

3.3.7. Attract and Kill—A Possible Solution?

The key issue is how the effect of an entomopathogen could be further enhanced for reliable control. One idea is the development of an attract-and-kill strategy that exploits the foraging behavior of herbivorous insects. This means the combination of a compound attracting the wireworms directly to the product and a killing compound that disposes of them effectively. Such attract-and-kill formulations could be used to enhance the effect of both EPN and EPF, as the wireworms are lured directly to the entomopathogen.

CO₂ is a known attractant for wireworms [74,176] and other soil insects [177,178]. Barsics et al. [179] summarized earlier research that demonstrated the existence of CO₂ perception and research on a shorter range working chemosensory sensillae in wireworms. Brandl et al. [172] developed an attract-and-kill system with an alginate capsule with yeast and starch producing CO₂ as an attractant, with a *Metarrhizium brunneum* strain as kill component; as a result, they were able to reduce tuber damage significantly when compared to the control in three out of seven field trials in potato. In four out of seven trials, the potato tuber damage appeared lower in the attract-and-kill when compared to kill

treatment, but differences were not significant. However, different application scenarios were tested, so the trials are not directly comparable. A resulting formulation is currently the only product in potato against wireworm damage in Germany (emergency registration, restricted acreage). According to Küppers et al. [171], a reduction in damage was achieved with this product at low-to-medium wireworm infestation.

Wireworms are also attracted to plant- or root-produced volatile aldehydes when they are actively foraging [180], similar to several other soil-inhabiting insect herbivores [181]. This or other organic plant compounds could be exploited for an attract-and-kill strategy. La Forgia et al. [182] encapsulated entomopathogenic nematodes with potato extracts as an attractant and feeding stimulant in alginate beads against the wireworm *Agriotes sordidus*. When compared to conventional EPN application and to beads containing only potato extract, the beads with both potato extract and *S. carpocapsae* or *H. bacteriophora* increased mortality rates, significantly only for the latter, indicating the importance of a suitable attractant for effective wireworm control. However, these are the first steps towards an attract-and-kill formulation, and it is possible that a combination of CO₂ and root volatiles may enhance the efficacy of the method even further.

Additionally, attract-and-kill strategies using entomopathogens (again *Metharizium brunneum* spores) as alternatives to chemical pesticides may also be used effectively to interfere with click-beetle populations and subsequent wireworm ones, as suggested by Kabaluk et al. [183]. This might be pursued by using modified pheromone traps that allow beetles to enter back and forth traps containing spore powder. This strategy does not require a 100% catch, or the vast majority of male beetles to be caught in a short space of time, since the killing agent would spread through the population, coming into increasing contact with both male and female adult beetles. At least in some click beetles, sex pheromones also perform as aggregation pheromones, and they can also attract significant numbers of females, as demonstrated for *A. sordidus*, *A. brevis*, and *A. ustulatus* [184–187]. This may be an additional pathway to increasing entomopathogen infections in click-beetle populations and further reducing wireworm pressure on crops.

3.3.8. Problem: Different Species of Wireworms

A general problem in biological control of wireworms is the involvement of several different wireworm species with mixed populations often at the same site [13,32,40,42,46,152,188–190]. When observing the differences in efficacy of a specific EPN or EPF strain against common wireworm species (e.g., [122,132,146]), it becomes clear that for biological control in a certain location, we need to know the wireworm species involved. This is not an easy task. Considerable time and expertise are needed for a reliable identification of wireworm species. Both the molecular method (PCR) and the morphological methods have their difficulties, but both produce reliable results for most individuals [13,39,40,72,191]. Additionally, recent molecular research suggested a possible occurrence of cryptic species in some North American wireworms [72,192], which may also affect the efficacy of a biological product. Furthermore, the activity pattern and damage potential of different wireworms in a crop may differ, which could affect the risk a certain species poses for a certain crop [35,153].

Early on, a specific key only for the Elateridae harming agriculture and horticulture needed to be established, as a major part of wireworms are not relevant in agriculture [193] and could be omitted. Keys for wireworms of economic importance only have been provided early in some countries [37,38,45]. Recently, a simple morphological key has been proposed for more common middle European genera in agricultural fields [41], which may be useful for farmers and plant protection service field workers without access to molecular methods. A final solution could be a combined product involving different strains of entomopathogens with sufficient growth at low temperatures, high efficacy against the commonest wireworm species in a region, and additionally an attractant source, applied in furrow at planting.

3.4. Naturally Derived Insecticides

Biocidal meals are practical options for controlling wireworm populations, both as prevention structural measures (wireworm population reduction at a suitable rotation period) and as rescue treatments just before the sowing of susceptible crop; after that, the occurrence of a wireworm density exceeding the threshold has been assessed [85]. They contain the same glucosinolate–myrosinase system described for biocidal cover crops (Section 3.1.1). Their potential can be considered comparable to that of chemical insecticides [85]. In laboratory [10] and pot trials [85], *Brassica carinata* seed meals caused a larval mortality higher than 80% and complete maize seedling protection. At large-field scale, both potato and maize crops have been effectively protected. In order to obtain successful practical results in the field, the same conditions described for biofumigant cover crops (Section 3.1.1) need to be fulfilled concurrently. Biocidal meals have become commercial products available for farmers, and practical implementation has already taken place.

3.5. Habitat Manipulation

Elaterid species are capable of exploiting both cultivated and uncultivated areas in the agricultural landscape [53]. Their movement from suitable habitats where populations thrive, i.e., source habitats such as grasslands, to vulnerable crops determines the colonization process and eventually crop damage. Thus, habitat connectivity in space and time [194,195] is a key driver of pest dispersal success in dynamic agricultural landscapes. Indeed, numerous studies have demonstrated that the spatial and temporal arrangement of land uses can provide a lever for action to control species abundances with regard to landscape compositional constraints (see for example [196–198]). Nevertheless, implementing such pest control strategies demands an extensive knowledge of pest biology and ecology, notably species-specific life traits such as life-cycle duration and dispersal ability.

The presence of uncultivated area in the field history or in the field vicinity [22–24,56,199] is clearly identified as a risk source in terms of wireworm infestation and/or crop damage; hence, it is often considered by farmers (e.g., managing the crop rotation within a field). More generally, while landscape context has been identified as a risk factor (Section 2.1), habitat manipulation remains underused. In their theoretical study, Poggi et al. [34] addressed the role of grassland in the field history, field neighborhood, and both. They have shown that species with a short life cycle are highly responsive to changes in land use, and that the neighborhood effect strongly relies on assumed dispersal mechanisms (random vs. directed movements). They also illustrated how the arrangement of grassy landscape elements in space and time can mitigate crop infestation by soil-dwelling pests, thereby emphasizing the relevance of managing grassland regimes. Thus, habitat manipulation may provide another component within an IPM approach.

4. Crop Damage Management

Wireworms are among the most destructive soil insect pests on potatoes and other crops, including corn and cereals (see Figure 5). Practices targeting limitation of damage despite substantial larval densities rely on identifying optimal planting and harvest conditions, protecting the sensitive crop with attractive companion plants, increasing seeding rates, and planting more tolerant cultivars.

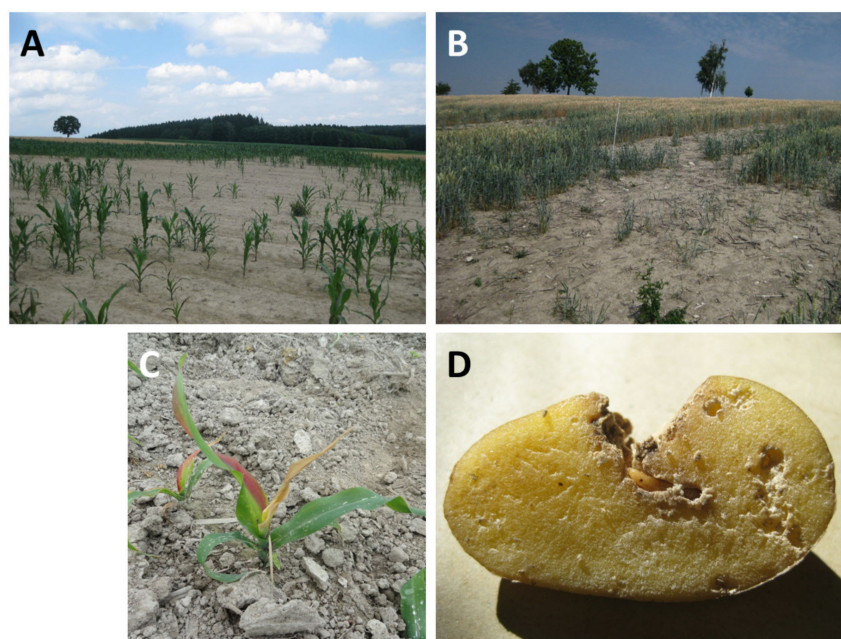


Figure 5. Illustration of crop damage and symptoms. (A) Damage in maize caused by mixed populations of *A. obscurus* and *A. lineatus*. (B) Damage in winter wheat caused by *A. sputator*. (C) Symptoms of wilting on maize small plants. (D) Damage on potato caused by *A. obscurus*. Photographs A, B, and D: JKI. Photograph C: Arvalis.

4.1. Cultural Control

4.1.1. Optimal Sowing and Harvest Timing

If substantial larval density is observed before maize planting, it is common to recommend delaying the sowing date as higher temperatures lead to shorter sensitive crop period, which should allow seedlings to resist damage. As regards planting time strategy, we have to consider that a population's capacity to damage sensitive plants varies with the season, e.g., in late spring, very high *A. ustulatus* populations do not damage maize stands because most of their larvae are in a non-feeding phase [9]. Therefore, adjusting planting times, when possible, to coincide with low pest populations or with non-damaging life stages can be effective. This recommendation cannot be generalized, since it is strictly depending on the species' life-cycle. Furlan et al. [23] showed that late sowing significantly increased damage risk on maize, mainly by *A. brevis* and *A. sordidus*, when compared with the ordinary sowing date. They explained this result by biological factors, as late sowing implies that most of the population is in the feeding phase due to higher temperatures accelerating larval molting, while small plants are still susceptible. Saussure et al. [52] also identified sowing date as a minor variable for explaining damage, contrary to the conclusions reached thus far. Poggi et al. [25], however, highlighted that soil temperature at maize sowing date influences damage. In potato production, recent studies in Germany and in Italy have shown that early harvest may reduce tuber damage [85,200]. Generally speaking, the less time potatoes stay in the field, the lower the wireworm damage risk; thus, short-cycle varieties may represent another synergic agronomic strategy.

4.1.2. Resistant Varieties

As for the variety/hybrid resistance to wireworm attacks, little is known and practically exploited. For example, recent achievements [201] suggest that there is potential for maize variety/hybrid tolerance/resistance to wireworms, but seed bags with this declared feature are unavailable. Likewise, less-susceptible-to-wireworm-feeding potato varieties have been identified, but based on the increasing potato damage claim from farmers reported by researchers [172], it seems that this agronomic strategy has not been exploited significantly. In potato production, several studies [202–205] highlighted reduced incidence

and severity of wireworm damage according to varieties. For example, Kwon et al. [205] tested 50 potato cultivars for resistance to several wireworm species. Injury rates varied between 80% and 96% in susceptible cultivars, and several varieties were found to be highly resistant.

4.2. Pest Behavior Manipulation: Feeding Pest as an IPM Strategy

Soil-dwelling wireworms are usually generalist herbivores, feeding on a wide range of species and usually feeding on most abundant species in their habitat [206]. They may also feed on animal prey [112] and be cannibalistic when larval density is too high for food resources [9,94]. The orientation of wireworms towards host plants is described as a three-step process [75,179]. First, wireworms orient towards carbon dioxide by klinotaxis. The next foraging step involves plant–root volatiles that allow host-specific recognition [207,208]; one example is aldehyde compounds influencing the ability of *A. sordidus* to locate barley roots [180]. The last step consists in the biting and the retention in the root systems containing asparagine, to which wireworms are sensitive, with the wireworms then remaining in the vicinity of the roots [209]. As their feeding phase only lasts 20% to 30% of their entire development [9,10,19], a promising and inexpensive pest management strategy could lie in feeding wireworms, thereby luring them away from the crop during the host susceptibility period [210]. Previous highly effective management strategies have tested pest behavior manipulation using trap cropping or companion plants.

4.2.1. Trap Crops

Trap crops are plants grown alongside the main crop in order to manipulate insect behavior to prevent pests from reaching the target crop [211]. If a trap crop can be found that lures pests, at least during sensitive growth periods of the main crop, sustainable and long-term management solutions can result. Hokkanen [211] describes approximately forty successful cases of trap crop strategies on several crops. As wireworms are very polyphagous [32], a wide range of trap crops are readily available. Despite limited larval mobility, wireworms have been found to be attracted and concentrated in trap crops placed around main crops [212,213]. In 2000, Vernon et al. [213] showed that trap crops of wheat, planted as trap crops a week before strawberry planting, can effectively reduce wireworm feeding and plant mortality. Landl and Glauningner [214] demonstrated the influence of peas as a trap crop on potatoes, and several studies have demonstrated that wheat intercropped with pea and lentil showed significantly less wireworm damage [215,216]. The attractiveness of trap crops, the timing of planting, and the space they occupy are major factors to consider before selecting and using a trap crop.

4.2.2. Companion Plants: Feeding Pests as an IPM Strategy

Companion planting is an agronomic strategy that sees the growing together of two plant species that are known to synergistically improve each other's growth. Companion plants can control insect pests either directly, by discouraging pest establishment, or indirectly, by attracting natural enemies that kill the pest. The ideal companion plant can be harvested, providing a direct economic return to the farmer in addition to the indirect value of protecting the target crop. In maize fields, it has been demonstrated that companion plants lure wireworms away from the crop and lead to a significant reduction (up to 50%) in damage, which is as effective as common chemical products (Belem 13kg/ha) [210,217,218]. Furthermore, meadow incorporation timing, just before crop seeding (e.g., maize), may protect crops from wireworm damage without any further intervention. This effect is due to the fact that soil-incorporated fresh meadow turf is a more attractive wireworm food source than seeds, emerging seedlings, and young plants [219].

5. Conclusions

Although many key aspects are still to be made available—the number of missing damage thresholds is astonishing—the bulk of available information allows us to immedi-

ately implement effective IPM strategies against wireworms. A practical IPM procedure for efficient wireworm management (including damage thresholds) has been described for maize in Europe [57,58]. This IPM procedure is currently implemented on thousands of hectares of cultivated land [7]. In Table 3, the IPM tactics and tools currently available for reducing the risk of wireworm crop damage to susceptible crops are classified according to their damage reduction potential and their current implementation status. “Already applied” practices with proven efficiency and practicability can be immediately implemented, while “under development” strategies are promising ones that still need large-scale evaluation and adaptations to variable practical conditions. “Under study” strategies comprise promising ongoing research, with no or negligible practical implementation, but they are being considered for possible future uses.

Table 3. Alternative strategies that can be applied to maintain wireworm density below damage thresholds according to results of continuous monitoring. One or more practices can progressively be applied to push back wireworm population levels. Under study: promising ongoing research but no or negligible practical implementation. Under development: limited practical applications; ongoing evaluations to adapt solution to variable practical conditions. Already applied: significant widespread implementation.

| Alternative Strategies | IPM Principles ** | Section Reference | Damage Reduction Potential | Applicability | Current Implementation |
|--|---|-------------------|---|---------------|------------------------|
| Continuous monitoring * integrated with risk assessment | P2: Monitoring (observation, forecast, diagnostics) | 2.1/2.2 | | High | Already applied |
| Continuous monitoring * integrated with risk assessment | P3: Decision based on monitoring and thresholds | 2.2.3 | | Medium | Already applied |
| Low risk rotation | P1: Prevention and suppression 1.2 Rotation | 3.1.1 | High | High | Already applied |
| Tillage | P1: Prevention and suppression 1.2 Rotation | 3.1 | High | High | Already applied |
| Biocidal cover crops | P1: Prevention and suppression 1.2 Rotation | 3.1 | Medium | Medium | Already applied |
| Identifying optimal planting/sowing and harvest conditions | P1: Prevention and suppression 1.3 Crop management and ecology | 3.1.2 | Medium/high (potato), low/medium others | High | Already applied |
| Biocidal materials | P4: Intervention 4.1 Non-chemical methods | 3.4 | Medium | Medium | Already applied |
| Larvae biocontrol using attract-and-kill device | P4: Intervention 4.1 Non-chemical methods | 3.3.7 / 3.3.8 | Medium/high | Medium | Under development |
| Tolerant varieties | P1: Prevention and suppression 1.3 Crop management and ecology | 3.1 | Medium/high (potato), low/medium others | Medium | Under study |
| Adult biocontrol using attract-and-kill device | P4: Intervention 4.1 Non-chemical methods | 3.3.7 / 3.3.9 | Medium | Medium | Under study |
| Larvae biocontrol using EPN | P4: Intervention 4.1 Non-chemical methods | 3.3.7 / 3.3.10 | Low/Medium | Medium | Under study |
| Habitat - landscape modifications | P1: Prevention and suppression 1.1 Combinations of tactics and multi-pest approach | 3.4 | Medium | Low/medium | Under study |
| Protecting the sensitive crop with attractive companion plants | P1: Prevention and suppression 1.3 Crop management and ecology | 4.2 | Medium | ? | Under study |

* Continuous population level assessment according to IPM principles and selection of fields with low wireworm density. ** From [15].

The IPM strategy level needed to continuously keep wireworm populations below damage thresholds, and the lowest possible cost can be pursued by implementing “flexible IPM packages”. These should be made up of two or more practices applied at the same time, provided that the different practices are compatible and that they have additional effects on wireworm population and crop-damage reduction. No incompatibilities between the strategies listed in Table 3 have been reported. The first fixed IPM practice, common to any flexible package, should be continuous pest population monitoring with low-cost tools,

such as pheromone traps (see Section 2.2.1), with complementary local bait trap wireworm monitoring before a susceptible crop seeding when needed (see Section 2.2.2).

IPM flexible packages may vary according to population levels assessed with continuous monitoring. Low-risk rotation should be implemented (see Section 3.1), in accordance with the prevalent wireworm species, including non-favoring crops and tillage when susceptible pest instars (eggs and young larvae) occur in the soil. If monitoring still assesses risky population levels and/or significant wireworm crop damage has been observed, other strategies should be added. These include the incorporation of biofumigant defatted seed meals (pellets) or biocidal plants. Farmers should find the package most suitable to their specific conditions and modulate package strategies as per wireworm population dynamics monitored by YATLORf traps (Table 3). Therefore, a general flexible IPM of wireworms should comprise two main phases: (1) a risk assessment that considers all the relevant agronomic and climatic characteristics that can be typically achieved by continuous monitoring of click-beetle populations with pheromone traps. Complementary wireworm field monitoring is advisable when risk assessment has identified the presence of risk factors and/or high beetle populations and/or previous wireworm crop damage; (2) the implementation of one or more of the practices listed in Table 3 in order to maintain or to restore wireworm populations below levels that cause significant damage to the susceptible crops in the planned rotation. Regardless of whether specific damage thresholds are available, farmers might find the IPM flexible package best suited to each homogeneous cultivated area on their farm by modulating preventative and rescue strategies (Table 3) so that susceptible crop damage is negligible. This should also require costs and the overall economic sustainability of alternative strategy implementation to be considered.

In order to make farmers comfortable with IPM implementation risks, insurance tools covering these risks may be particularly useful and supported by legislation (mutual funds). Mutual fund compensation is commensurate with the financial resources of the fund. The fund stock is increased by savings in forecast costs and covers risks that private insurance companies currently do not, e.g., climatic adversities such as flooding and damage by wild animals and pests, just before and after the emergence of arable crops. The first implementations are underway in Italy and the results are promising [220].

While important advances have been recently made, many gaps remain in the setting up of a complete and efficient IPM framework to deal with wireworm issue in crops. Indeed, significant progress is still needed on many aspects of our knowledge. The association between wireworm density and harmfulness to various crops in different conditions is still missing for several species. This impedes the establishment of precise, verifiable thresholds for each crop \times wireworm species in the various cultivated contexts and areas. Knowledge on behavioral ecology of adults remains highly fragmentary, notably concerning their dispersal (distance, orientation) or their choice of egg-laying site. Progress would be useful if we are to better understand colonization processes and to address wireworm risk at landscape scale. Abiotic and biotic soil parameters (e.g., organic matter content) that favor the survival and development of larvae should be specified in order to identify suppressive soils (i.e., soils that maintain wireworm populations at low levels naturally). This would mainly require assessing the main natural causes of larval mortality, including parasitism and predation, and a better understanding of larval trophic ecology and life-cycle. In terms of agricultural sciences, studies on various promising practices, including tilling, use of biofumigants, or setting up companion plants, should be fostered. In addition, despite some promising preliminary results, varietal tolerance/resistance has, to date, received little attention. Finally, holistic decision-support tools for the implementation of IPM should be rendered available to farmers. Eventually, precise and verifiable targets for IPM implementation for each crop \times wireworm species in the various cultivated areas [7] should be identified, with any relevant socio-economic aspects also being considered.

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