Chapter 2

The Journey of the Potato Tuberworm Around the World

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Additional information is available at the end of the chapter

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Abstract

Potato (*Solanum tuberosum* L.) production is challenged by many factors including pests and diseases. Among insect pests, *Phthorimaea operculella* Zeller (Lepidoptera: Gelechiidae), known as the potato tuber worm or potato tuber moth, is considered one of the most important potato pests worldwide. *Phthorimaea operculella* is a cosmopolitan pest of solanaceous crops including potato, tomato (*Solanum lycopersicum* L.), and other important row crops. Adults oviposit in leaves, stems, and tubers; immature stage mines leaves causing foliar damage, but most importantly, burrows into tubers rendering them unmarketable. Currently, pest management practices are effective in controlling *P. operculella,* but the effectiveness depends on many factors that will be discussed later in this chapter. Each section includes up-to-date information related to *P. operculella* biology, ecology, and control, including origins, host range, life cycle, distribution, seasonal dynamics, and control methods.

Keywords: *Phthorimaea operculella*, lepidoptera, gelechiidae, moth, pest management, solanaceous, IPM, tubermoth

1. Introduction

Potato (*Solanum tuberosum* L.) is the fourth major food crop around the world after rice (*Oryza sativa* L.), wheat (*Triticum* spp.), and maize (*Zea mays* L.). Potato is rich in vitamins, minerals, proteins, antioxidants, essential amino acids, and carbohydrates [1–4], and it is an important part of many cultures diet around the world. Indians from Peru were the first ones to cultivate potatoes around 8000–5000 BC; by the early 1500s, when the Spaniards arrived to South America, they brought first potato plants to Europe, and eventually, potatoes were genetically improved and grown, and nowadays, the crop is utilized worldwide [5].

Potato production is challenged by many factors including pests and diseases. Depending on where potato production occurred, aphids (*Macrosiphum euphorbiae* Thomas and *Myzus persicae* Sülzer), leafhoppers, potato psyllids (*Bactericera cockerelli* Šulc), beetles (*Leptinotarsa decemlineata* Say), and moths can have a tremendous effect on the crop. *Phthorimaea operculella* Zeller (Lepidoptera: Gelechiidae), also known as the potato tuber worm or potato tuber moth (**Figure 1**), is considered one of the most important potato pests worldwide [6–14]. *Phthorimaea operculella* is a cosmopolitan pest of solanaceous crops including potato, tomato (*Solanum lycopersicum* L.), and other important row crops [15–19]. Adults oviposit in leaves, stems, and tubers; the immature stage mines leaves, (**Figure 2**) but most importantly, larvae burrow into tubers rendering them unmarketable (**Figure 3**); unfortunately, outbreaks are still difficult to predict. Pest management practices are effective in controlling *P. operculella*

Figure 1. *Phthorimaea operculella* Zeller adult. Photo credit: Oregon State University, Extension and Experiment Station Communication (Ketchum).

Figure 2. *Phthorimaea operculella* Zeller larva. Photo credit: Oregon State University, Extension and Experiment Station Communication (Ketchum).

Figure 3. *Phthorimaea operculella* Zeller tuber damage. Oregon State University. Irrigated Agricultural Entomology Program (Rondon).

but the effectiveness depends on the response time to pest infestation, resources available, and pest management practitioner experience. This chapter includes a compilation of up-to-date information related to *P. operculella* biology, ecology, and control, including origins, host range, life cycle, distribution, seasonal dynamics, and control methods.

2. *Phthorimaea operculella* as an agricultural pest around the world

Phthorimaea operculella was first reported as pest-affecting tubers in South America in the early 1900s [20, 21]. Foliar damage does not usually result in significant yield losses [20]; however, reduce marketability and damage due to tuber infestation can be significant in nonrefrigerated storage conditions [22]. For instance, in the Middle East, *P. operculella* infestation can range between 1 and 65% [23, 24], while in India, *P. operculella* is responsible for about 1–13% and 70–100% infestation in the field and storage, respectively [25–29]. In Ethiopia, *P. operculella* is responsible for 9–42% yield loss [30]; Lagnaoui et al. [31] indicated that yield loss in storage could be up to 100% where no temperature and/or humidity control is possible.

2.1. Scientific nomenclature of the potato tubeworm

The taxonomic tree of *P. operculella* is illustrated in **Figure 4**. This insect belongs to the Phylum Arthopod, Class Insecta, Order Lepidoptera, Sub-Order Glossata, Super Family Gelechioidea, Family Gelechiidae, and Sub-Family Gelechiinae. *Phthorimaea operculella* was described in 1873 as *Bryotropha* and then *Gelechia operculella* [32]. The genus was revised in 1902 and 1931 and assigned to the genus *Phthorimaea* in 1964 by Meyrick [33], Povolny [34], and Povolny and Weissman [35]. In the old literature, *P. operculella* can be found as *Gnorimoschema operculella, Lita operculella, Lita solanella, P. solanella, and P. terrella*; more recently as *Scrobipalpa operculella, Scrobipalpus solanivora*, and *S. solanivora*; until finally recognized as *P. operculella* [36].

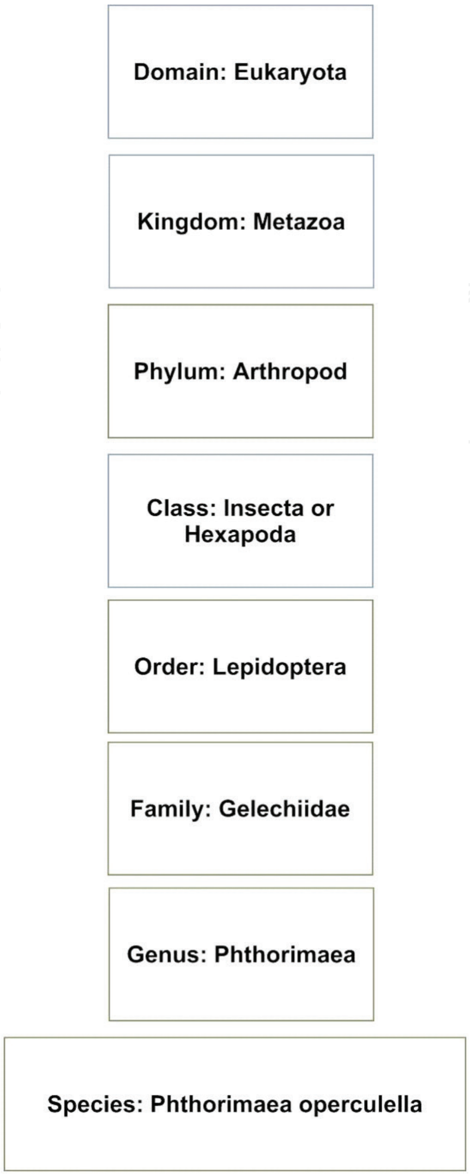

Figure 4. Taxonomical tree of *Phthorimaea operculella*. Photo credit. Oregon State University. Irrigated Agricultural Entomology Program (Rondon).

Although in the Entomological Society of America database, the common name of *P. operculella* is potato tuberworm [37], other recognized regional names are listed in **Table 1**. Currently, two other species of Gelechiidae moths are known as "tuber worms," *Tecia solanivora* (Povolny), restricted to Central and Northwest South America known as the Central American potato tuberworm or Guatemalan potato moth, and *Symmestrischema plaesiosema* (Turner), found in South America, Southeast Australia, and Philippines [19, 38]. This chapter will focus on the *Phthorimaea* species.

2.2. Distribution

Currently, *P. operculella* can be found in all potato production areas in tropical and subtropical countries in South, Central, and North America, Africa, Australia, and Asia [14, 40–42].

Language	Common names
English	Potato moth; potato tuber worm; stem end grub; tobacco leafminer; tobacco split worm; tobacco splitworm
Spanish	Gusano de la papa; gusano del tubérculo de la papa; minador común de la papa; minador de la hoja del tabaco; oruga barrenadora del tallo; palomilla de la patata; polilla de la papa; polilla de la patata
French	Teigne de la pomme de terre
German	Kartoffelmotte
Italian	Tignola della patata
Danish	Kartoffelmol
Dutch	Aardappel-knollenruspje
Hebrew	Ash habulbusin

Table 1. Common names of ***Phthorimaea operculella*** Zeller [36, 39].

Phthorimaea operculella is the single-most significant insect pest of potato (field and storage) in North Africa, Asia, and the Middle East [43, 44]. In the mid-1800s, *P. operculella* was reported in Tasmania, New Zealand, and Australia [45]. In South Central Asia, *P. operculella* was introduced in 1906 to Bombay, India, apparently from Italy [46]; but by the mid-1900s, *P. operculella* became widely distributed in all potato regions in India. In 1913, *P. operculella* was first reported in the USA [14, 47–50]; at present, *P. operculella* is present in most USA potato production regions [14, 51]. The first report in China took place in 1937, when Chen found *P. operculella* larvae in tobacco (*Nicotiana tabacum* L.) plants in the Liuzhou City in Guangxi province [52–54]. In the mid-1970s, *P. operculella* was introduced to Iraq [24, 55], and by the early 1980s, it was found in Russia [56]. From 2002, *P. operculella* has emerged as a problem in the Bologna providence in northern Italy [57]. To our knowledge, there are few studies describing the population structure of *P. operculella* around the world that could explain *P. operculella* distribution. In the USA, Medina and Rondon [58] suggested that geographical barriers such as the Appalachian Mountains in North America might act as a geographic barrier isolating *P. operculella* sub-populations. *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae), a close relative of *P. operculella*, is a serious pest of tomatoes in Europe, Africa, western Asia, South America, and Central America and can sometimes be taxonomically confused with *P. operculella* [59, 60].

2.3. Host range

Phthorimaea operculella is primarily a pest of potato but also can be found in other solanaceous crops and weeds (**Table 2**). There is only one report unconfirmed of *P. operculella* in sugar beet [61]. Das and Raman [16] reported alternate hosts representing 60 plant species, both cultivated and wild. Most of the hosts belong to the Solanaceae family, while others belong to the Scrophulariaceae, Boraginaceae, Rosaceae, Typhaceae, Compositae, Amaranthaceae, and Chenopodiaceae.

Phthorimaea operculella can be found in all crops and weeds listed above; however, field studies have shown that *P. operculella* only reproduce when feeding on potato, tomato, sugar

Host Common name	Scientific name	Family
Potato	*Solanum tuberosum*	Solanaceae
Eggplant, aubergine	*Solanum melongena* L.	Solanaceae
Bell pepper	*Solanum annuum* L.	Solanaceae
Tomato	*Solanum lycopersicum* L.	Solanaceae
Black nightshade	*Solanum nigrum* L.	Solanaceae
Silver leaf nightshade	*Solanum elaeagnifolium* Cav.	Solanaceae
Chili pepper	*Capsicum frutescens* L	Solanaceae
Tobacco	*Nicotiana tabacum* L	Solanaceae
Cape gooseberry	*Physalis peruviana* L.	Solanaceae
Field ground cherry	*Physalis mollis* D.	Solanaceae
Prickly nightshade	*Solanum torvum* Sw.	Solanaceae
Jimson weed	*Datura stramonium* L.	Solanaceae
Gooseberry	*Physalis angulate* L.	Solanaceae
Angel's tears	*Brugmansia suaveolens* Bersch	Solanaceae
	Fabina, Lycium, Hyoscyamis, Nicandra	Solanaceae
Sugarbeet	*Beta vulgaris var. saccharifera*	Amaranthaceae

Table 2. List of common hosts of *Phthorimaea operculella* Zeller [28, 61–66].

beet, and eggplant [16, 28, 47, 61, 67–71]. In the western USA states, *P. operculella* was found to feed and reproduce only in potatoes [14, 50]. Early behavior of first instars is critical for establishing in a suitable host plant [72]; thus, not surprisingly, food source availability and quality are critical in *P. operculella* establishment and success [14, 50]. A pattern in the diet of many groups of herbivorous insects is that related species tend to feed on related co-evolutionary plants; however, do not dismiss the adaptability of the insect taxa [73]. A great example of this statement is the co-evolution of the potato crops and the Colorado potato beetle, *Leptinotarsa decemlineata* Say [74]. All instars of *P. operculella* can potentially survive in volunteer potatoes or in the soil [50, 75–77] and have high adaptability to cold acclimation, cooling rate, and heat stress [78].

3. Biological and ecological aspects

3.1. Biology

Phthorimaea operculella has four life stages: adult, egg, larva, and pupa. Development, survival, and reproductive rates vary considerably in relationship to host quality and availability [79].

3.1.1. Adults

Adults are small moths (approximately 0.94 cm long) with a wingspan of approximately 1.27 cm. Forewings have 2–3 dark dots on males and an "X" on females [14, 29, 50, 80, 81] (**Figure 5**). Both pairs of wings have characteristic-fringed edges. Early literature considered that adults were poor fliers [9, 14, 15, 82]; however, recent studies have shown that they can fly for over 5 hours or up to 10 km nonstop [83]. Krambias [84] and Foley [83] indicated that *P. operculella* cannot fly at wind speeds in excess of about 5–6 m/s. Moths are active at temperatures between 14.4 and 15.5°C; at around 11.1°C, they can crawl through soil cracks or burrow short distances through loose soil. In Oregon, *P. operculella* was observed searching for tubers at temperatures close to 5°C. [85]. Copulation can take place only 16–20 hours after adult emergence; the duration of copulation ranges between 85 and 200 minutes [28, 86, 87]. Adults can live for 1–2 weeks [77]. Adults are normally inactive during the day and oviposition occurs at night [68, 69, 88–90]. Adults do not oviposit in the soil close to tubers if potato foliage is available [14, 89, 91]. Eggs laid and their longevity are directly related to their nutrition [14, 90, 92, 93], and age of male appears to play an important role in the ability to mate [94]. Selection of plants for oviposition is determined by the physical nature of plant surface and by chemical factors that are detected only when females enter in contact with the host [61]. Meisner et al. [70] showed that oviposition is stimulated by ethanolic extracts and I-glutamic acid released from potato peels. Chemical cues are mainly responsible for host selection; olfactory detection of plant volatiles may elicit the female to find the best host for her offsprings [95].

3.1.2. Eggs

Eggs are ≤0.1 cm spherical, translucent when freshly laid turning white or yellowish to light brown after 1–2 hours. In the field, females lay their eggs on foliage, soil and plant debris, or

Figure 5. *Phthorimaea operculella* female (left) and male (right). Photo credit. Oregon State University. Irrigated Agricultural Entomology Program (Rondon).

exposed tubers [14, 50]; however, foliage was the preferred oviposition substrate [72]. There are discrepancies related to number of eggs per batch [24, 77, 96, 97]. For instance, Gubbaiah and Thontadarya [28] indicated that in the field, females laid eggs singly and rarely in groups of 3–5 eggs on either side of the leaf but close to the mid-rib. In the storage (~7.2°C), eggs were laid singly or in groups of 3–15 near the eye buds. Regarding distribution of eggs in plants, eggs can be widely distributed with greater numbers found around the base of the plants [89]; in confinement, *P. operculella* oviposits in groups close to eye buds [85]. Incubation period could range from 5 to 34 days [65], 4–5 days [98], 2.3 and 7.2 days at 33.3 and 20.9°C, respectively [24], 3–10 days [24, 63, 99, 100]. Attia and Mattar [68] reported 36°C as the upper critical temperature at which no eggs were laid.

3.1.3. Larvae

Larvae are usually cream to light brown reddish with a characteristic brown head. Mature larvae (0.94 cm long) may have a pink or greenish color; thorax has small black points and bristles on each segment [77]. No sexual dimorphism is observed until the third larval stage where initial sexual structures are visible; in the 4th larval stage, males are different from females where males have two elongated yellowish testes in the 5th and 6th abdominal segment [29]. Moregan and Crumb [101] reported 15–17 days for the larval period; Graft [20] and Trivedi and Rajagopal [65] reported 13–33 days, and Van der Goot [98] reported 14 days. Larvae feed on leaves throughout the canopy but prefer the upper foliage; larvae mine the leaves, leaving the epidermal areas on the mid/lower leaf surface unbroken [14]. Larvae move via cracks in the soil to find tubers, thus exposed tubers are pre-disposed to *P. operculella* damage [14, 50]. Larvae close to pupation drop to the ground and burrow into the tuber to complete its life cycle, making a swirl silk cocoon pupating on soil surface or in debris. Especially in warm dry climates, the larva can attack potato plants in field and storage causing great damage [96, 99].

3.1.4. Pupae

Occasionally, *P. operculella* pupae can be found on the surface of tubers (**Figure 6**), most commonly associated with tuber eyes [50]. *Phthorimaea operculella* pupae (0.84 cm long) are smooth and brown and often enclosed in a covering of fine residue that protects them from low temperatures and helps them endure the winter [76]. There is a clear distinction between male and female pupae. Rondon and Xue [81] evaluated the "scar" and the "width" method. Using the "scar" method, males could be recognized by the distance between the incision located between the 8th and 9th abdominal segment and the tip of the abdomen; there is also a gradual change in color eye pigmentation, which can help estimate the age of the pupae. Based on eye pigmentation, pupae are classified into newly formed pupa (yellowish in color, 1–2 day old pupae), followed by early red (3 day old), middle red (4 day old), late red, and black eye pupa (5–6 day old) [29, 81, 86, 102, 103]. Some studies suggest that the pupal period is not fixed but depends on the temperature at which the larvae grew [104]. Moregan and Crumb [101] reported 6–9 days as pupal period; Graft [20] reported 13–33 days; and Van der Goot [98] observed 14–17 days. Studies in the western USA indicated that *P. operculella* adults can potentially emerge from soil at depths up to 10 cm [76]. Once adults emerge, mating occurs, and within a few hours, females seek a potential host to lay their eggs.

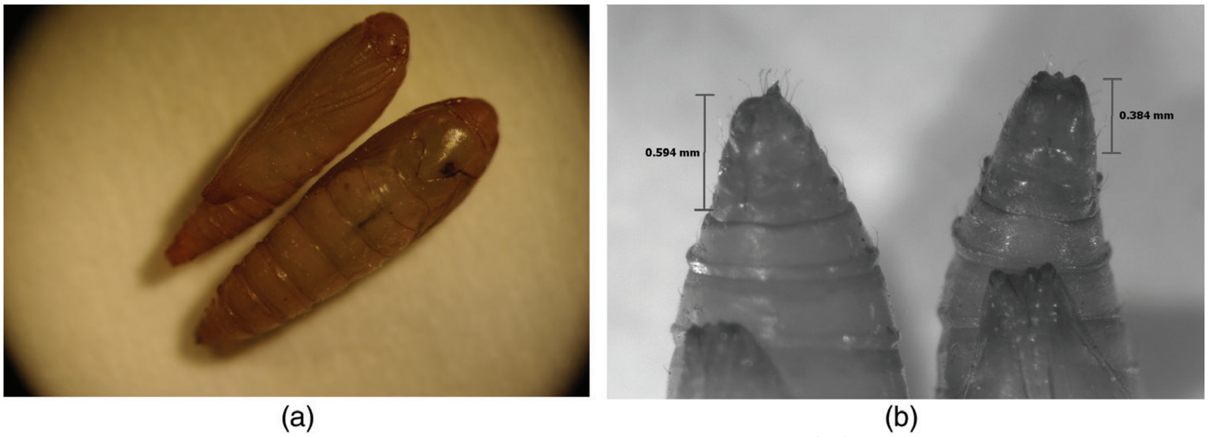

Figure 6. *Phthorimaea operculella* pupa and scar. (A) Female (right) and male (left); (B) Female (left); male (right).Photo credit: Oregon State University. Irrigated Agricultural Entomology Program (Rondon).

3.2. Life table

Phthorimaea operculella can complete several generations per year. Chittenden reported two generations of *P. operculella* in summer and a third generation in storage in the USA [105]; generally speaking, *P. operculella* is not a problem in the USA under controlled conditions [14]. In 2006, several potato storage controlled units were visited (n = 50), and only one had severe *P. operculella* infestation (Rondon personal observation). The infested unit stored tubers that came heavily infested from the field. Van der Goot [98] reported 6–8 generations a year in tropical regions; French [106] reported 2 generations in Australia, first in the winter and the second one on stored tubers; Graft [20], Trivedi and Rajagopal [65], and Sporleder et al. [107] reported 3–4 generations in Chile and the southern USA; Mukherjee [108] reported 13 generations per year in India, and Al-Ali et al. [24] reported 12 generations in Iraq. Recently, pheromone trapping in Bologna, Italy, where researchers integrated temperature dependent developmental time models, showed that *P. operculella* completed two generations throughout the potato-growing season; the remaining generations developed in the noncrop season [57]. This information suggests a correlation between geographical location, presence or absence of food source, and *P. operculella* generations per year [14]. Sporleder et al. [109] indicated that locations with one crop per season will have 2–3 generations per year (e.g., western USA), while locations with year-round crops like in India will have several generations per year [108].

3.3. Damage

Luscious, healthy, disease-free plants attract more *P. operculella* than wilting, nonirrigated plants [110]. Once *P. operculella* reaches a field, distribution of foliar damage tends to be nonrandom [7, 9, 111, 112] and more severe on the edges of the field facing the prevailing winds in a band parallel to the edge [9]. Larval density in foliage and tubers is higher at the margins of the field than in the center [18], a typical characteristic of pests that move from nearby areas [9, 17, 82]. Drier conditions in plants on field edges caused by wind and solar radiation leads to more *P. operculella* females looking for oviposition sites [17, 18, 70, 113]. Research shows that moths are able to forage beyond 100–250 m from center of origin [114]. In the western USA, most of the potatoes are vine-killed right before harvest; thus, when foliage is gone, *P. operculella* readily moves to nearby green fields or directly down to the tubers [50, 51].

3.4. Developmental thresholds

Phthorimaea operculella developmental threshold has been widely studied [29, 68, 88, 107, 109, 115, 116]. Developmental thresholds are necessary in order to establish best timing of control methods [97, 107, 117]. Differences in temperature for *P. operculella* development suggest the remarkable adaptation of this insect [14, 68, 69, 76, 107, 115]. Temperature-dependent development can be useful in forecasting occurrence and population dynamics of pests. Golizadeh and Zalucki [118] determined that the lower temperature threshold and thermal constant of immature stage were estimated to be 11.6°C and 338.5 degree days. A degree day is a measurement of heat units over time calculated from daily maximum and minimum temperatures; the minimum temperature at which insects' first start to develop is called the "lower developmental threshold," or baseline and the maximum temperature at which insects stop developing is called the "upper developmental threshold" or cutoff [119]. Golizadeh et al. [120] determined the average fecundity of females ranged from 45.3 eggs (at 16°C to 117.3 eggs (at 28°C); net reproductive rate (R_0) ranged from 12.8 (at 16°C) to 43.2 (at 28°C); and mean generation time (T) decreased with increasing temperatures from 61.0 days (at 16°C) to 16.2 days (at 32°C). These data suggest the close relationship between insect and abiotic factors.

3.5. Temperature affects life parameters of *P. operculella*

The developmental response of insects to temperature is important in understanding the ecology of insect life histories [121]. Temperature has an effect on geographical distributions, population dynamics, and management of insects [121]. For instance, studies by Langford and Cory [96] indicated that low temperatures retard and cause temporary cessation of *P. operculella* development not only physiologically but also due to the destructive effect of low temperatures on the food supply. Eggs exposed to 1.6–4.4°C for 4 months failed to hatch [96, 122]. Langford and Cory [96] indicated that outbreaks of *P. operculella* in Virginia in 1925 and 1930 coincided with hot and dry years, and the intensity of infestation varies in proportion to rainfall and humidity. Early studies in Maryland and Virginia [123, 124] indicated that *P. operculella* pupae can survive "short" constant sub-freezing temperatures. Several other authors reported that larvae and pupae could potentially survive frost [122, 125, 126]; other studies indicated that all life stages of *P. operculella* were killed by exposure to −6.6°C for 24 hours [96, 122]. Early studies by Langford in 1934 reported that *P. operculella* survived temperatures ranging from −11.6 to −6.6°C, but lengthy exposures to low temperatures were fatal to all stages. Trivedi and Rajagopal [65] found that pupae were extremely tolerant to low temperatures; however, Langford and Cory [96] indicated that full-grown larvae survived better at low temperatures [96]. In a manipulative study to determine how growth stage (egg, larva, or pupa) and soil depth affected the potential for winter survival, Dŏgramaci et al. [76] found that egg survival was reduced after 1 month of exposure to low temperatures; larvae were able to survive up to 30 days at 20-cm soil depth, while tubers at the surface buried at 6 cm were frozen; the pupal stage showed a greater tolerance to winter conditions (average −2°C) than the egg or larval stages, surviving up to 91 days of exposure. Hemmati et al. [78] studied the effect of cold acclimation. According to their study, super cooling points from 1st and 5th instar larvae, pre-pupae, and pupae were −21.8, −16.9, −18.9, and −18.0°C, respectively. Cold acclimation (1-week at 0 and 5°C) did not affect super cooling for 4–5th instar larvae, pre-pupae, and pupae. Also, LT_{50}s (lower lethal temperature for 50% mortality) for 1st and 5th instar larvae, pre-pupae, and pupae were −15.5, −12.4, −17.9, and −16.0°C, respectively. They concluded that cold acclimation resulted in a significant decrease in mortality of all developmental stages, and heat hardening also affects cold tolerance. A relatively recent study by Golizadeh et al. [120] determined that tubeworm failed to survive at 36°C during the egg period, and adult longevity was negatively correlated with temperature and the longest adult longevity was observed at 16°C.

3.6. Other parameters affecting *P. operculella*

Other parameters such as elevations and latitude seemed to play a role in *P. operculella* incidence [116]. Locations with higher spring, summer, or fall temperatures were associated with increased trapping rates in most seasons; in the western USA, trapping data from spring 2004 to fall 2005 showed that *P. operculella* males were present every week except in mid-January, with the greatest *P. operculella*/per trap occurring in December at around −0.09°C [50, 116, 127]; also, "warm" winters may also account for high *P. operculella* populations the following season [14, 116]. Similar observations were recorded in other insect species [128, 129]. In Israel, *P. operculella* first generation reached its peak in May or June (late spring, early summer) [18], and overlapping generations reached high numbers close to harvest which seems to be a characteristic of nondiapausing insects that continuously have access to host plants [18, 35, 104, 107, 110, 130, 131].

4. Monitoring

4.1. Pheromones

Phthorimaea operculella male moths are attracted to pheromones that are concentrated chemicals of the female "scent" impregnated in a rubber septum in the center of a sticky liner placed in delta traps [14]. According to Herman et al. [13], two chemicals have been identified as the main component of *P. operculella* sex pheromone: (E4, Z7)-tridecadienyl acetate (PTM1) [132] and (E4, Z7, Z10)-tridecatrienyl acetate (PTM2) [133]; chemicals have been synthesized, blended, and tested, and modifications are commercially used [134, 135]. Some other insects including other Gelechiidae moths could be trapped in the sticky liners; thus, liners should be changed once a week and lures should be changed once a month [50]. Pheromone traps are used to monitor populations in the field to help time insecticide applications [13]. Several authors found a positive relationship between the number of trapped adults and the density of larvae in the foliage and tuber [10, 75, 136]. Growers in areas impacted by *P. operculella* are encouraged to monitor insect using pheromone traps [50]; this has been an activity conducted in western USA states since 2005 (https://agpass.maps.arcgis.com/apps/webappviewer/index.html?id=8f3577c883ab4ac58f262b4cd04ff569). Horne [137] used three methods to collected *P. operculella*: random and selected leaf samples and pheromone traps, concluding that random sampling of leaves did not always give adequate estimates as particular life stages could be overestimated or excluded from samples. In the western USA, pheromones traps are widely used [50]. Current recommendations include sampling at least 10 plants per field or section of the field; individual plants may be examined for the presence or absence of *P. operculella*; near 55% of the mines are found in the upper third of the potato plants are they are not easily to find; set at least 1 pheromone trap per 123 acres [50].

4.2. Action thresholds

Although treatment levels have not been established for *P. operculella*, California recommends a threshold of 15–20 moths per trap per night as a general threshold level [138] and 8 moths per trap per night for Oregon [139]. Keep in mind that *P. operculella* numbers vary from field to field and from area to area; thus, it is recommended to tailored management recommendations on field(s) specific information [50, 51]; and standard thresholds should be used exclusively as a reference.

4.3. Trapping

Kennedy [140], Bacon et al. [141], Raman [135], Salas et al. [142], and Tamhankar and Hawalkar [143] have reported results using different type of traps. In New Zealand, Herman et al. [13] tested water traps, which caught the greatest number of *P. operculella* per trap as compared to "DeSIRe" delta shaped sticky traps, "A traps" (cylinder-shaped), and funnel traps. Herman et al. [13] concluded that delta traps were the most suitable for commercial use. Coll et al. [18] presented information regarding pheromone traps plus poison bait placed on the ground at 50 m intervals in single rows with positive results. Based on Herman et al. [13] findings, the recommendation in the western USA has been to place at least one delta trap per potato field, beginning after canopy closure [50]; recent recommendations include placing four traps per field [14]. Soil type has an effect on number of moths caught per trap; thus, in sandy soils of Israel, pheromone traps caught almost twice as many moths than in loess fields [18].

5. Controlling *P. operculella*

Key aspects of the biology and ecology of *P. operculella* are important in selecting management practices to control this pest [14, 139]. Considering that most of the economic damage by this insect occurs when the insect infests the tubers, we should focus in early control of the pest [14]. For instance, deeper seed planting, hilling the rows, irrigation, and early harvest are a few of the methods suggested to prevent tuber infestation [10, 122, 126, 139, 144]. The use of chemicals, however, is still the main foundation of *P. operculella* control worldwide [139, 145–147]. It is advisable to check with your local extension or government agencies to review which pesticides are allowed to use in your region. Always read the labels and follow the manufacturers' recommendations.

5.1. Cultural control

Cultural methods reported to reduce *P. operculella* population include the elimination of cull piles and volunteers, timing of vine-kill, soil moisture at and after vine-kill, time between desiccation and harvest, rolling hills and covering hills, and cultivar selection [50, 139, 144]. In Tunisia, practices like deep seeding, hilling up, early harvest, irrigation until harvest, good sorting of tubers at harvest, and rapid harvesting prevent tuber infestation [148, 149]. In Sudan, planting date, planting depth, hilling-up, irrigation intervals, and mulching on insect infestation and on the greening of tubers in the field were studied [150]. Ali [150] indicated that tuber shape and skin characteristics had no effect on the degree of *P. operculella* infestation; early planting date resulted in fewer insect damage and greater yield compared to crops planted 3 weeks later; greater depth of planting and more frequent hilling-up significantly lowered infestation levels; light irrigation every 4 days and mulching with neem (*Azadirachta indica* L.) incorporated before harvest were the most effective treatments.

5.1.1. Elimination of volunteer potatoes and cull piles

The growth of volunteer potatoes is a serious problem because of the competition with current season crops but also for sanitary reasons [151] (**Figure 7**). For instance, Aarts and Sijtsma [152] indicated that volunteer potatoes can overgrow crops such as maize or sugar beets at planting, but lesser once established. In South Africa, *P. operculella* is described as a significant pest before harvest and during storage; and since eggs, larvae, or pupae can survive on volunteer potatoes, they represent a source of infestation for the following season [153, 154]. Besides volunteer potato elimination, cull piles should be removed to reduce overwintering stages which are a source of next years' population [75]. Certainly, in western USA states, volunteer potatoes can serve as a "green bridge" of numerous insect pests.

5.1.2. Rolling potatoes

Research has found that rolling of potato hills in sandy soil caused soil to slough off the hill, which resulted in increased *P. operculella* damage; obviously, this is not recommended in areas with sandy soils [50, 144]. Covering hills with 3–5 cm of soil immediately after vine-kill, which can be accomplished with a rotary corrugator, has been shown to significantly reduce tuber infestation [50, 144, 155]; however, it is not necessarily a common practice in the region. Others showed that exposed tubers are more prone to *P. operculella* infestation [9, 156]. They indicated that tuber infestation occurred 2–4 weeks before harvest and all infested tubers were covered with no more than 3 cm of soil.

5.1.3. Vine-killed

Tubers naturally mature as the potato plant senesces but tuber maturation can be artificially induced by killing the potato vines mechanically, chemically, or with a combination of both [14].

Figure 7. Volunteer potato in a crop field. Photo credit: Oregon State University. Irrigated Agricultural Entomology Program (Rondon).

Empirical observations suggest that all these activities have an impact on the level of *P. operculella* infestation [14]. Field observations support the principle that *P. operculella* prefer green foliage to tubers for oviposition and feeding; thus, when foliage starts to decline, tubers are exposed, and therefore, infestations naturally increase; thus, the time between desiccation and harvest is crucial. The longer tubers are left in the field after desiccation, the greater the likelihood of tuber infestation [14, 50, 51]. Intuitively, tubers exposed or close to the soil surface are at high risk for *P. operculella* injury. In the Columbia Basin of Oregon, our recommendation includes to maintain more than 5 cm of soil over the tubers especially at the end of the season or after vine-killed [50].

5.1.4. Soil moisture

Phthorimaea operculela female moths favor dry soil for oviposition [70, 113]. Larval survivorship increased with decreasing soil moisture [113]. Then, keeping the soil moist to avoid cracks in the soil, particularly at the end of the season when vines are drying, reduces *P. operculella* tuber infestation. Rondon et al. [50], Clough et al. [155], and Rondon and Hèrve [139] researches have shown that irrigating daily with 0.25 cm through a center pivot irrigation system from vine kill until harvest decreased *P. operculella* tuber damage without increasing fungal or bacterial diseases. How water may decrease *P. operculella* movement? Since water closes soil cracks, reducing tuber access, *P. operculella* possibly perish from lack of oxygen in the soil due to water saturation, and/or their mobility is reduced by wet soil, decreasing their ability to move and find a tuber.

5.2. Biological control

Phthorimaea operculella is a relatively minor pest of potatoes in South America, probably due to the existence of a diverse complex of natural enemies attacking this pest [157]. Biological control, which is the use of living organisms to control pest populations, can have an environmental impact while controlling pest populations [158]. There are several organisms including parasitoids, and pathogens such as fungi or viruses, that have been used successfully to control *P. operculella* (**Table 3**).

5.2.1. Parasitoids

In general, Callan [159] indicated that the "newcomers" normally achieved better control than the "native" natural enemies, possibly caused by the long-term coevolution or adaptation between the relevant species at different trophic levels in South America. Thus, exploration for more parasitoids in the large parts of South America, Central America, and Mexico could be a promising way to improve the parasitoid-based biocontrol. Many parasitoids have been introduced mainly from South America, the area for the origin of *P. operculella* [153, 160]. Since 1918, biological control efforts attempted to introduce *Bracon gelichiae* L. to France from the Americas [36]. *Trichogramma* and *Copidosoma* species are among the most widely used parasitoids used to control *P. operculella* but with mixed results [69, 161–164]. *Copidosoma koehleri* Blanchard and *Bracon gelechiae* Ashmead have been used successfully in South America and Australia, respectively [66]; however, in Israel, *C. koehleri*, an encyrtid polyembryonic, did not reduce *P. operculella* populations, accounting only for 4–5% *P. operculella* larval reduction; similar results were found by Berlinger and Lebiush-Mordechi [165, 166] in Israel. In Italy, Pucci et al. [167] also found modest results. While several biotic and abiotic conditions in the eco-niche determine the population establishment and effectiveness of parasitoids [12], the reduction of human interference through reducing insecticide application is crucial for the parasitoid(s) establishment and performance [153]. Also, the effect of resources like flowering for parasitoids establishment is important [162]. In a laboratory study, when *C. koehleri* females were deprived of hosts for the first 5 days of their adult lives, neither the number of eggs laid nor longevity was significant affected [162]. Kfir [168] studied the fertility of *C. koehl*eri compared to *Apanteles subandinus* L. under the effect of humidity in South Africa, concluding that low humidity is detrimental for the survivorship of this species. Choi et al. [169] and Aryal and Jung [170] reported *Diadegma fenestrale* L. found for the first time in Korea and accounted for 20–30% parasitism. In Sardinia, *Diadegma turcator* Aubert, and *Bracon nigricans* L., *B. properhebetor* L., and *Apantele*s spp. were also found attacking *P. operculella* [171].

Scientific name	Parasitizing stage	Place	Reference
Agathis gibbosa	Larvae	USA	Odebiyi and Oatman [172]
			Flanders and Oatman [173]
Agathis unicolor	Larvae	South America	Lloyd [157]
Apanteles litae	—	—	Lloyd [174]
Apanteles subandinus	Larvae	South Africa	Watmough et al. [153]
		South America	Franzmann [175]
		Australia	Horne [176]
		India	Rao and Nagaraja [177]
		Zimbabwe	Mitchell [178]
Apanteles scutellaris	Larvae	India	Rao and Nagaraja [177]
		USA	Flanders and Oatman [173]
Bracon gelechiae	—	India	Rao and Nagaraja [177]
Bracon hebator		India	Divakar and Pawar [179]
Campoplex haywardi	Larvae	USA	Leong and Oatman [180]
Campoplex phthorimaeae	—	—	Flanders and Oatman [173]
Chelonus blackburni	Eggs, larvae	India	Choudhary et al. [181]
Chelonus contractus	Eggs	France	Labeyrie [182]
Chelonus curvimaculatus	Eggs	South Africa	Watmough et al. [153]
Chelonus kellieae	Larvae	USA	Flanders and Oatman [173]
			Powers [183]
Chelonus phthorimaea	Larvae	USA	Powers [183]
Copidosoma desantis	Eggs	Australia	Franzmann [175]
Copidosoma koehleri	Larvae	Australia	Horne [176]
		South Africa	Keasar [184]
		Israel	Cruickshank and Ahmed [185]
		South America	Kfir [186]
		Italy	Lloyd [157]
		Zimbabwe	Mitchell [178]
Copidosoma uruguayensis	Larvae	South Africa	Watmough et al. [153]
		South America	
Diadegma compressum	—	—	Flanders and Oatman [173]
Diadegma molliplum	—	—	Lloyd and Guido [174]
Diadegma stellenboschense	Larvae	South Africa	Watmough et al. [153]
Elasmus funereus	Larvae	Australia	Franzmann [175]
Habrobracon gelechiae	Larvae	US Pacific Northwest	Rondon 2007 [50]
Microchelonus curvimaculatus	Larvae	Australia	Franzmann [175]
Microgaster phthorimaea	—	—	Flanders and Oatman [173]

Scientific name	Parasitizing stage	Place	Reference
Nepiera fuscifemora	—	—	Flanders and Oatman [173]
Orgilus californicus	—	—	Flanders and Oatman [173]
Orgilus lepidus	Larvae	Australia	Franzmann [175] Horne [176]
Orgilus parcus	Larvae	South Africa	Watmough et al. [153]
Orgilus jenniae	Larvae	USA	Flanders and Oatman [187]
Parahormius pallidipes	—	—	Flanders and Oatman [173]
Pristomerus spinator	—	—	Flanders and Oatman [173]
Sympiesis stigmatipennis	—	—	Flanders and Oatman [173]
Temelucha minuta	Larvae	Australia	Franzmann [175]
Temelucha picta	Larvae	South Africa	Watmough et al. [153]
Trichogramma brasiliensis	Eggs	India	Harwalkar and Rananavere [188]
Zagrammosoma flavolineatum	—	—	Flanders and Oatman [173]

Table 3. List of parasitoids that control *Phthorimaea operculella* Zeller. Compiled by Y. Gao.

5.2.2. Predators

The role of generalist predators such as *Orius* spp. [189], hymenopteran [190], *Dicranolaius* spp. [191], phytoseiid [192], *Chrysoperla* spp. [193], *Agistemus* [194], and others predators present in potato ecosystems has not been widely studied [18]. *Geocoris* sp. (Hemiptera: Miridae) was seen as a potential *P. operculella* predator in Nepal [195].

5.2.3. Biorationals

Other potential biological control agents include nematodes and entomopathogens. The nematode of the genus *Hexamermis, Steinernema,* and *Heterorhabditis* are suggested to exert significant control on *P. operculella* [196, 197]. *Steinernema feltiae*, *S. bibionis*, *S. carpocapsae,* and *Heterorhabditis heliothidis* were used in laboratory experiments in Russia with promising results [198]. Kakhki et al. [199] found that the higher the concentration (0, 75, 150, 250, 375, and 500 js/mL) of *S. carpocapsae* and *H. bacteriophora,* the higher is the mortality in both larval and pre-pupal stages. Fungal entomopathogens such as *Beauveria bassiana* and *Metarhizium anisopliae* have been isolated from *P. operculella* larvae, extracted, and used as bio-insecticides causing *P. operculella* death at a rate higher than 80% [200–204]. Back in 1967, a granulovirus was found and reported as a new record [205]; the following years, the granulovirus was isolated and collectively named *Phthorimaea operculella granulovirus* (PhopGNV). They are well known for efficiently controlling and preventing *P. operculella* in storage [206]. Since first reported, GNV has been tested for pest control in the fields in South America and Australia [206]. Arthurs et al. [207] evaluated PoGV and *Bacillus thuringiensis subsp. kurstaki* for control of *P. operculella* in stored tubers with limited efficacy.

5.3. Chemical control

5.3.1. Field

Traditional chemical control targeting mainly larvae and adults is well documented [208, 209]. Back in the 1970s, azinphos-ethyl and endosulfan were effective against foliage mining [7]. Others reported thiacloprid, quinalphos, and diflubenzuron as effective [210, 211]. Rondon et al. [50] provided some information related to pesticide use in the USA. However, potential strategies to improve chemical control are also being investigated. Mahdavi et al. [212] studied the insecticidal activity of plant essential oils including the insecticidal and residual effects of nanofiber oil and pure essential oil of *Cinnamomum zeylanicum* L. under laboratory conditions; fumigant toxicity was evaluated on different growth stages (egg, male, and female adults) of *P. operculella* with encouraging results. Similarly, Mahdavi et al. [213] tested *Zingiber officinale* Roscoe, demonstrating the relative effectiveness of additional means of control. Tanasković et al. [214] revised the effect of several plants as bio-insecticides to suppress *P. operculella*.

5.3.2. Storage

In the USA, *P. operculella* is not a problem during storage, since storage occurs under controlled conditions of temperature and humidity [14]. However, in other parts of the world, *P. operculella* can cause significant damage during storage. Moawad and Ami [215] and Abewoy [30] reported that *P. operculella* causes serious damage to stored potato through its larval tunneling and feeding, which can lead to secondary infection by fungi or bacteria. During storage, the damaged tubers become unsuitable for human consumption; moreover, the adult moth flies from the infested tubers in the storage and from neglected warehouses or farms back to the fields, where it causes pre-harvest infestation. Granulovirus was found to efficiently control *P. operculella* in Colombia and was used as a biopesticide in storage conditions [206]. Early on, Raman and Booth [216], Raman et al. [217], and Lal [218, 219] indicated that *P. operculella* could be reduced by covering tubers with *Lantana camara* L., *L. aculeate* L., or *Eucalyptus globulus* Labill foliage. Niroula and Vaidya [220] reported good control using *Minthostachys* spp., *Baccharis* spp., *L. neesiana,* and *Artemisia calamus* L.; Sharaby et al. [221] tested peppermint oils, camphor, eugenol, and camphene in Egypt.

5.4. Resistance: plant versus insect resistance?

Host plant resistance enables plants to avoid, tolerate, or recover from pest infestations [222, 223]. Genome diversity of tuber-bearing potato presents a complex evolutionary history that complicates domestication in the cultivated potato [224]. Currently, abundant evidences in other insect-plant interactions systems exist, especially the defensive chemical compounds. In contrast, the amount of information to improve potato genotypes against *P. operculella* is still lacking [225]. Cultivated potatoes have more than 100 tuber-bearing relatives native to the Andes of southern Peru; among them, *Solanum chiquidenum* L. and *Solanum sandemanii* L. for instance, which are highly resistant to *P. operculella,* damage in tubers [226]. The nutritional value of the host is an important resistance factor limiting normal growth and development of *P. operculella* [227]. Moreover, some potato hybrids can inhibit oviposition, while surviving larvae had higher mortality and slower feeding rates than those larvae reared on foliage of cultivated potatoes [228]. An improved investigation of the mechanisms for the traits associated with the tuber and foliage resistance and the introduction of these traits into commercial varieties may be an effective way to enhance the plant resistance against *P. operculella*. Golizadeh et al. [229] tested the resistance of six potato cultivars; also, Rondon et al. [85] studied potato lines, some of which exhibit promising results for controlling mines and number of larvae in potato tubers [77]. An earlier study by Rondon et al. [85] confirmed that tubers of the transgenic clone Spunta G2 were resistant to *P. operculella* damage. Spunta G2 was developed in the early 2000s [230, 231]. In recent years, plants have received genes that encode toxic proteins to resist against insects [232, 233]. Thus, researchers like Fatehi et al. [234] evaluated the effect of wheat extracts against digestive alpha-amylase and protease activities against *P. operculella*; those enzymes are important digestive enzymes used during the feeding process. Inhibition of enzymes could potentially help us reduce or stop *P. operculella* feeding. Also, radiation to induce sterility of *P. operculella* males has also been studied [235–237].

6. Conclusions

Phthorimaea operculella is considered one of the most important potato pests worldwide. It is a cosmopolitan pest of solanaceous crops including potato, tomato, and other important row crops. Based on *P. operculella* biology, ecology, including its relationship with the potato crop well thoughout pest management practices, can keep the pest under control. The effectiveness of control methods will depend on the response time to pest infestation, resources available, and also, pest management practitioner experience. This chapter includes up-to-date information related to *P. operculella* that we anticipate will be useful to growers, fieldmen, and producers that face the challenges imposed by this pest.

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