A Review of the Host Plant Records of *Phthorimaea absoluta* (=*Tuta absoluta*) (Lepidoptera: Gelechiidae)[1]

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Abstract *Phthorimaea absoluta* (=*Tuta absoluta*) (Meyrick) (Lepidoptera: Gelechiidae), an invasive pest native to South America, poses a severe threat to solanaceous crops, particularly tomatoes (*Solanum lycopersicum* L.). Other researchers have often attempted to claim *P. absoluta* as a polyphagous pest and expanded its host plant list based on unverified observations without evaluating whether the plant could support the completion of the life cycle. Such an approach has led to the inclusion of numerous non-Solanaceae families as hosts, creating ambiguity about the pest's true host range. To address this issue, we reviewed published articles and extracted host plant records from 63 species across the Solanaceae and non-Solanaceae families. Host plants were assessed for their suitability to support complete, partial, or no life cycle of *P. absoluta*. Our findings revealed that only a specific subset of host plants, predominantly within the Solanaceae, support the complete life cycle of this pest, defining its true host range as an oligophagous herbivore. In contrast, other recorded host plants permit only partial development or fail to sustain larval survival. A notable finding is the mismatch between female oviposition preferences and larval development, resulting in variability in host plant usage across genera such as *Nicotiana* and *Datura* and even within *Solanum*. These discrepancies may stem from geographic, chemical, and ecological factors. Inconsistent methodologies and limited data pose significant challenges to clarifying the pest's true host range. This review highlights the need for life cycle data to clarify the host range of *P. absoluta*. By addressing these gaps, this study advances host specialization theories and supports future research on invasive pests.

Key Words host plant preference, growth performance, oviposition, Solanaceae

Phthorimaea absoluta (=*Tuta absoluta*) (Meyrick) (Lepidoptera: Gelechiidae), commonly known as the South American tomato pinworm, is a highly invasive pest native to South America. Over the past few decades, this species has exhibited remarkable dispersal capacity, establishing itself as a significant agricultural threat across Europe (Desneux et al. 2011, Sridhar et al. 2014), Africa (Bastola et al. 2020, Mansour et al. 2018), and Asia (Campos et al. 2017, Pandey et al. 2023). The devastating impact of *P. absoluta* on solanaceous crops, particularly tomatoes (*Solanum lycopersicum* L.), has made it a critical subject in the study of invasive insect pests (Biondi et al. 2018, Desneux et al. 2010).

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Monophagous herbivores are characterized by their diet, which is restricted to one or more plant species within the same genus (Döring and Hoffmann 2004). In contrast, oligophagous herbivores consume plants from two or more genera within a single family or closely related families, and polyphagous herbivores exhibit an even broader feeding spectrum, feeding on plants across multiple families (Cates 1980, 1981). Although *P. absoluta* is frequently classified as an oligophagous herbivore (Aksoy and Kovanci 2016, Goudarzvand Chegini and Abbasipour 2017, Kumari et al. 2014, Mangrio et al. 2023, Prasannakumar et al. 2021) because of its predominant association with Solanaceae and the significant influence of these host plants on its fitness, survival, and geographical distribution (Cherif and Verheggen 2019, Desneux et al. 2010, Silva et al. 2021, Uzun et al. 2015), host plant records have been extended to include other families, such as Fabaceae (Idriss et al. 2020, Ingegno et al. 2017b), Malvaceae (Bawin et al. 2016, Cherif and Verheggen 2019), Amaranthaceae (Pandey et al. 2023, Portakaldali et al. 2017, Xian et al. 2017), Convolvulaceae (Bawin et al. 2015), Cucurbitaceae (Ingegno et al. 2017a, Ingegno et al. 2017b), and Geraniaceae (Cherif and Verheggen 2019). This wide host range has created ambiguity in categorizing *P. absoluta* as either oligophagous or polyphagous. The host range of an insect herbivore is defined as the range of host plant species capable of supporting the insect's complete life cycle development (Schaffner 2001). However, identification of host plant species of herbivore insects based on inconsistent and variable host plant records often stems from a mismatch between female oviposition preferences and larval developmental success (Menken et al. 1992, Potter et al. 2012, Rojas et al. 2018). Although efforts to document the host plant range of *P. absoluta* are valuable, they often neglect critical aspects such as variations in the pest's life cycle and developmental patterns across different host plant species. Without robust evidence confirming the full developmental success of phytophagous insects on these extended host plant species, inclusion of these plants within the insect's host range could be misleading (Lee et al. 2023, Schaffner 2001, Thompson 1988). Key questions, such as the causes of mismatches between female oviposition preferences and larval developmental success, or the reasons for variations in host plant utilization even among closely related species within the same genus remain unresolved. These gaps impede the accurate identification of optimal host plants and the precise delineation of the pest's host range.

Resolution of discrepancies is essential for accurately defining the optimal hosts and host range of *P. absoluta* (Arnó et al. 2019, Idriss et al. 2020, Sylla et al. 2019). Such insights are pivotal for devising effective management strategies and mitigating the pest's impact on global agriculture. In this present study, we addressed these critical gaps by integrating life cycle data with ecological and evolutionary insights to refine the understanding of the host range of *P. absoluta*. By unraveling the underlying factors driving discrepancies between oviposition choices and larval performance, we hoped to enhance the accuracy of host identification and provide a more robust framework for predicting host plant suitability.

Materials and Methods

Data collection. We gathered research and review articles by using a keyword-based search strategy with the terms "oviposition preference test," "*Tuta* *absoluta,*" "larval performance," "Solanaceae host plants," and "host adaptation." We curated 113 research and review articles from more than 65 journals, supplemented by host plant records obtained from the EPPO Global Database (2024). To categorize and visualize the information related to the life cycle and development of *P. absoluta,* we used the approach shown in Table 1. We were able to also collect host plant records of 63 host plant species from 26 countries through available literature (Table 2).

Assessment process. All host plant species names were indicated according to the APG IV system (Angiosperm Phylogeny Group 2016) and GBIF (2024) (Table 2). To investigate mismatches between female *P. absoluta* oviposition preferences and larval developmental success and the variabilities in host plant preferences within the same genus, we compiled a comprehensive summary of host plant records. Our analysis emphasized key factors such as host plant family, species, life cycle, developmental patterns, references, study type, and the geographical distribution of studies (Table 2). Most host plant records were derived from observational data or cross-references to previous studies. Consequently, we focused exclusively on records that provided detailed insights into the life cycle and development of *P. absoluta*. These records were drawn from reviews, laboratory and greenhouse experiments, and field experiments. Field experiments were particularly considered when they included data such as the number of larval mines, larval density assessments, and confirmations of developmental status. Studies that did not directly measure larval development based on life table parameters but inferred developmental success based on significantly higher numbers of larval mines or larvae per mine were categorized as supporting optimal development. Conversely, lower numbers of mines or larvae per mine were interpreted as indicative of partial development, consistent with the methodologies of Sylla et al. (2019) and Ghaderi et al. (2018).

Data analysis and visualization. A figure was created to represent the summarized data on life cycle and developmental patterns across all 63 documented host plant species (Fig. 1). We also examined discrepancies between female oviposition preferences and larval developmental success, focusing specifically on host plant utilization within the Solanaceae (42 host species) (Fig. 2) and non-Solanaceae families (21 host species) (Fig. 3). To explore inconsistencies in host plant utilization within the same genus, we created a visual representation of oviposition preferences and larval developmental success in *P. absoluta* with a particular emphasis on the genus *Solanum,* the largest genus within the Solanaceae family (Hilgenhof et al. 2023). This analysis included 23 host species (Fig. 4) from the genus *Solanum*. All illustrations were created with data extracted from the literature; percentages were rounded to the nearest whole number for improved clarity and visualization.

Results

Among the 63 host plant species, 24% of the species ($n = 15$) supported the complete development of *P. absoluta,* whereas for the majority (76%) there was not sufficient evidence of optimal development of this insect. However, for 43% of the host plant species ($n = 27$) documented by previous authors sufficient

Table 1. Categories of the host plant records of *Phthorimaea absoluta* extracted from literature based on completeness of the information.

Category	Oviposition	Development of Larvae	Adult Emergence
Complete life cycle observed	Yes	Yes	Yes
Partial life cycle observed	Yes	Yes	No
	Yes	No	No
No oviposition observed	No		
No information on life cycle and development	Lack of information to be included in any of the above categories, which requires future investigations		
Inconsistent	Include host plant species with variable information as indicated in previous records		

information was lacking, which could influence these numbers in future investigations (Fig. 1).

Of the 42 host plant species of the family Solanaceae, 36% ($n = 15$) supported the complete development of *P. absoluta,* whereas for the majority (64%) there was not sufficient evidence of its optimal development. However, for 36% of the host plant species ($n = 15$) documented by previous authors sufficient information was lacking, which could influence these numbers in future investigations (Fig. 2).

Of the 21 non-Solanaceae host plant species, none supported the complete development of *P. absoluta,* and for 43% there was not sufficient evidence of its optimal development. However, for 57% of the host plant species ($n = 12$) documented by previous authors sufficient information was lacking, which could influence these numbers in future investigations (Fig. 3).

Of the 23 host plant species from the genus *Solanum,* for 44% ($n = 10$) of those documented by previous authors sufficient information was lacking, which could influence these numbers in future investigations (Fig. 4).

Discussion

Host plant preferences of female moths. Previous studies on host plant selection provide evidence supporting the oviposition preferences of female *P. absoluta*. These results highlight the fact that female oviposition preferences significantly influence larval survival; early stage larvae face considerable challenges when switching to alternative host plants, rendering them highly vulnerable to unfavorable conditions (Awmack and Leather 2002, Galdino et al. 2015, Gripenberg et al. 2010, Leather and Awmack 2002). Galdino et al. (2015) found that oviposition preferences in *P. absoluta* females are influenced by climatic conditions and the presence of natural enemies. Host selection by female *P. absoluta* is

Table 2. Published information on life cycle and development of *Phthorimaea absoluta* on various plants, which are listed alphabetically by genus.

Family	Species	Life Cycle Information	Reference	Study type	Study Location
Solanaceae	*Atropa belladonna* L.	Complete life cycle observed	Bawin et al. (2015)	Lab experiment	Belgium
			Cherif and Verheggen (2019)	Review	Belgium
	Capsicum annuum L.	Oviposition observed; no completion of the life cycle	Silva et al. (2021)	Greenhouse and lab experiments	Brazil
			Sylla et al. (2019)	Lab and field experiments	France and Senegal
			Guenaoui et al. (2010)	Field experiment	Spain
			Uzun et al. (2015)	Greenhouse and lab experiments	Turkey
			Portakaldali et al. (2017)	Field experiment	Turkey
		No oviposition or completion of the life cycle	Osman et al. (2021)	Lab experiment	Egypt
			Smith et al. (2018)	Field experiment	Tanzania
	Capsicum chinense Jacquin	Oviposition observed; no completion of the life cycle	Silva et al. (2021)	Greenhouse and lab experiments	Brazil
	Capsicum frutescens L.	Oviposition observed; no completion of the life cycle	Idriss et al. (2020)	Lab and field experiments	Sudan
	Datura ferox L.	No oviposition observed.	Galarza (1984)	Greenhouse and lab experiments	Argentina
			Abbes et al. (2016)	Lab experiment	Tunisia
			EPPO (2024)	Global database	
			Cherif and Verheggen (2019)	Review	Belgium
	Datura quercifolia Kunth	No information on life cycle and development	Pandey et al. (2023)	Review	Nepal
			Tarusikirwa et al. (2020)	Review	Botswana

Table 2. Continued.

Family	Species	Life Cycle Information	Reference	Study type	Study Location
	Datura stramonium L.	Oviposition observed; no completion of the life cycle	Arnó et al. (2019)	Greenhouse and lab experiments	United States
		Complete life cycle observed	Bawin et al. (2015)	Lab experiment	Belgium
			Cherif and Verheggen (2019)	Review	Belgium
		No oviposition or completion of the life cycle	Abbes et al. (2016)	Lab experiment	Tunisia
			Smith et al. (2018)	Field experiment	Tanzania
	Lycium chilense Miers ex Bertero	No information on life cycle and development	EPPO (2024)	Global database	
			Cherif and Verheggen (2019)	Review	Belgium
	Lycium halimifolium Miller	Complete life cycle observed	Bawin et al. (2016)	Greenhouse and lab experiments	Belgium
			Cherif and Verheggen (2019)	Review	Belgium
	Lycopersicon puberulum Philippi	No information on life cycle and development	Cherif and Verheggen (2019)	Review	Belgium
	Nicandra physalodes (L.) Gaertner	No oviposition observed	Bawin et al. (2016)	Greenhouse and lab experiments	Belgium
			Cherif and Verheggen (2019)	Review	Belgium
	Nicotiana glauca Graham	Complete life cycle observed	EPPO (2024)	Global database	
			Cherif and Verheggen (2019)	Review	Belgium
	Nicotiana rustica L.	Complete life cycle observed	Bawin et al. (2016)	Greenhouse and lab experiments	Belgium
			Cherif and Verheggen (2019)	Review	Belgium
	Nicotiana tabacum L.	Partial life cycle observed	Bawin et al. (2016)	Greenhouse and lab experiments	Belgium
			Cherif and Verheggen (2019)	Review	Belgium

Table 2. Continued.

Family	Species	Life Cycle Information	Reference	Study type	Study Location
		Main host of development (complete development)	Pandey et al. (2023)	Review	Nepal
			Aslan and Birgücü (2022)	Greenhouse and lab experiments	Turkey
			Jiang et al. (2023)	Greenhouse and lab experiments	China
	Physalis angulata L.	No information on life cycle and development	Xian et al. (2017)	Review	China
	Physalis peruviana L.	No information on life cycle and development	Pandey et al. (2023)	Review	Nepal
			Cherif and Verheggen (2019)	Review	Belgium
			Tropea Garzia (2009)	Field experiment	Italy
	Physalis viscosa L.	No oviposition observed	Cherif and Verheggen (2019)	Review	Belgium
			Galarza (1984)	Greenhouse and lab experiments	Argentina
	Salpichroa origanifolia (Lamarck) Baillon	No oviposition observed	Cherif and Verheggen (2019)	Review	Belgium
			Galarza (1984)	Greenhouse and lab experiments	Argentina
	Solanum aculeatissimum Jacquin	Complete life cycle observed	Silva et al. (2021)	Greenhouse and lab experiments	Brazil
	Solanum aethiopicum L.	Complete life cycle observed	Sylla et al. (2019)	Lab and field experiments	Senegal
	Solanum americanum Miller	Complete life cycle observed	Silva et al. (2021)	Greenhouse and lab experiments	Brazil
			Smith et al. (2018)	Field experiment	Tanzania
	Solanum anguivi Lamarck	No information on life cycle and development	Retta and Berhe (2015)	Review	Ethiopia
	Solanum dulcamara L.	Complete life cycle observed	Bawin et al. (2016)	Greenhouse and lab experiments	Belgium
			Cherif and Verheggen (2019)	Review	Belgium

Table 2. Continued.

Family	Species	Life Cycle Information	Reference	Study type	Study Location
	Solanum gilo Raddi	Complete life cycle observed	Silva et al. (2021)	Greenhouse and lab experiments	Brazil
	Solanum habrochaites S. Knapp and D.M.Spooner	Complete life cycle observed	Silva et al. (2021)	Greenhouse and lab experiments	Brazil
	Solanum lycopersicum L.	Complete life cycle observed	Silva et al. (2021)	Greenhouse and lab experiments	Brazil
			Arnó et al. (2019)	Greenhouse and lab experiments	United States
			Abbes et al. (2016)	Lab experiment	Tunisia
			Sylla et al. (2019)	Lab and field experiments	France and Senegal
			Zhang et al. (2021)	Field experiment	China
			Smith et al. (2018)	Field experiment	Tanzania
			Cuthbertson et al. (2013)	Greenhouse experiment	United Kingdom
			Polat et al. (2016)	Greenhouse experiment	Turkey
			Cherif et al. (2013)	Greenhouse, laboratory and field experiments	Tunisia
			Idriss et al. (2020)	Lab and field experiments	Sudan
			Desneux et al. (2010)	Review	
			Cherif and Verheggen (2019)	Review	Belgium
			Kanle Satishchandra et al. (2019)	Lab and field experiments	India
			Negi et al. (2018)	Lab and field experiments	India
			Pereyra and Sánchez (2006)	Lab experiment	Argentina
			Mutamiswa et al. (2017)	Lab and field experiments	Botswana
			Osman et al. (2021)	Lab experiment	Egypt
			Tumuhaise et al. (2016)	Lab and field experiments	Uganda

Table 2. Continued.

Family	Species	Life Cycle Information	Reference	Study type	Study Location
			Ishtiaq et al. (2020)	Lab and field experiments	Pakistan
			Zhang et al. (2020)	Field experiment	China
			Mukwa et al. (2021)	Lab and field experiments	DR of Congo
			Biondi et al. (2018)	Review	
			Desneux et al. (2011)	Review	
			Gabol et al. (2014)	Field experiment	Pakistan
			Aslan and Birgücü (2022)	Greenhouse and lab experiments	Turkey
			Bhat and Bajracharya (2019)	Lab experiment	Nepal
			Sanda et al. (2018)	Review	Nigeria
			Portakaldali et al. (2017)	Field experiment	Turkey
			Konan et al. (2022)	Field experiment	Côte d'Ivoire
			Lee et al. (2024)	Lab and field experiments	South Korea
	Solanum tuberosum L.	Complete life cycle observed	Silva et al. (2021)	Greenhouse and lab experiments	Brazil
			Abbes et al. (2016)	Lab experiment	Tunisia
			Bawin et al. (2015)	Lab experiment	Belgium
			Sylla et al. (2019)	Lab and field experiments	France and Senegal
			Zhang et al. (2021)	Field experiment	China
			Smith et al. (2018)	Field experiment	Tanzania
			Cherif and Verheggen (2019)	Review	Belgium
			Biondi et al. (2018)	Review	
			Zhang et al. (2020)	Field experiment	China
			Pereyra and Sánchez (2006)	Lab experiment	Argentina

Table 2. Continued.

Family	Species	Life Cycle Information	Reference	Study type	Study Location
			Osman et al. (2021)	Lab experiment	Egypt
			Kanle Satishchandra et al. (2019)	Lab and field experiments	India
			Desneux et al. (2010)	Review	
			Negi et al. (2018)	Lab and field experiments	India
			Jiang et al. (2023)	Greenhouse and Lab experiments	China
			Bhat and Bajracharya (2019)	Lab experiment	Nepal
			Desneux et al. (2011)	Review	
			Portakaldali et al. (2017)	Field experiment	Turkey
	Solanum macrocarpon L.	No information on life cycle development	Pandey et al. (2023)	Review	Nepal
	Solanum melongena L.	Complete life cycle observed	Silva et al. (2021)	Greenhouse and lab experiments	Brazil
			Zhang et al. (2021)	Field experiment	China
			Smith et al. (2018)	Field experiment	Tanzania
			Cherif and Verheggen (2019)	Review	Belgium
			Sylla et al. (2019)	Lab and field experiments	France and Senegal
			Osman et al. (2021)	Lab experiment	Egypt
			Kanle Satishchandra et al. (2019)	Lab and field experiments	India
			Ingegno et al. (2017a)	Greenhouse experiment	Italy
			Ingegno et al. (2017b)	Greenhouse experiment	Italy
			Aslan and Birgücü (2022)	Greenhouse and lab experiments	Turkey

Table 2. Continued.

Family	Species	Life Cycle Information	Reference	Study type	Study Location
			Jiang et al. (2023)	Greenhouse and lab experiments	China
			Bhat and Bajracharya (2019)	Lab experiment	Nepal
			Negi et al. (2018)	Lab and field experiments	India
			Portakaldali et al. (2017)	Field experiment	Turkey
		Significantly lower occurrence of larvae in field	Idriss et al. (2020)	Lab and field experiments	Sudan
	Solanum muricatum Aiton	Complete life cycle observed	Ingegno et al. (2017a)	Greenhouse experiment	Italy
			Ingegno et al. (2017b)	Greenhouse experiment	Italy
			Cherif and Verheggen (2019)	Review	Belgium
			Negi et al. (2018)	Lab and field experiments	India
	Solanum nigrum L.	Complete life cycle observed	Silva et al. (2021)	Greenhouse and lab experiments	Brazil
			Arnó et al. (2019)	Greenhouse and lab experiments	United States
			Bawin et al. (2015)	Lab experiment	Belgium
			Smith et al. (2018)	Field experiment	Tanzania
			Campos et al. (2021)	Greenhouse experiment	France
			Cherif and Verheggen (2019)	Review	Belgium
			Abbes et al. (2016)	Lab experiment	Tunisia
			Idriss et al. (2020)	Lab and field experiments	Sudan
			Zhang et al. (2021)	Field experiment	China
			Portakaldali et al. (2017)	Field experiment	Turkey
			Biondi et al. (2018)	Review	
	Solanum paniculatum L.	Oviposition observed; no completion of the life cycle	Silva et al. (2021)	Greenhouse and lab experiments	Brazil

Table 2. Continued.

Family	Species	Life Cycle Information	Reference	Study type	Study Location
	Solanum saponaceum Dunal	No information on life cycle development	Silva et al. (2021)	Cross Reference	Brazil
	Solanum sarrachoides Sendtner	Complete life cycle observed	Arnó et al. (2019)	Greenhouse and lab experiments	United States
	Solanum sisymbriifolium Lamarck	No information on life cycle development	Cherif and Verheggen (2019)	Review	Belgium
	Solanum bonariense L.	No information on life cycle development	Cherif and Verheggen (2019)	Review	Belgium
	Solanum dubium Fresenius	No information on life cycle development	Cherif and Verheggen (2019)	Review	Belgium
	Solanum elaeagnifolium Cavanilles	No information on life cycle development	Cherif and Verheggen (2019)	Review	Belgium
	Solanum lyratum Thunberg	No information on life cycle development	Cherif and Verheggen (2019)	Review	Belgium
	Solanum scabrum Miller	No information on life cycle development	Pandey et al. (2023)	Review	Nepal
	Solanum villosum Miller	No information on life cycle development	Pandey et al. (2023)	Review	Nepal
	Withania somnifera (L.) Dunal	Oviposition observed; no completion of the life cycle	Subramani et al. (2021)	Greenhouse experiment	India
Amaranthaceae	*Amaranthus spinosus* L.	No information on life cycle development	EPPO (2024)	Database	
			Cherif and Verheggen (2019)	Review	Belgium
			Pandey et al. (2023)	Review	Nepal
	Amaranthus viridis L.	No information on life cycle development	Xian et al. (2017)	Review	China
	Beta vulgaris L. var. *vulgaris* L.	No oviposition observed	Bawin et al. (2016)	Greenhouse and lab experiments	Belgium
			Cherif and Verheggen (2019)	Review	Belgium

Table 2. Continued.

Family	Species	Life Cycle Information	Reference	Study type	Study Location
	Chenopodium album L.	No oviposition observed	Portakaldali et al. (2017)	Field experiment	Turkey
			Bawin et al. (2016)	Greenhouse and lab experiments	Belgium
			Cherif and Verheggen (2019)	Review	Belgium
	Chenopodium bonus-henricus L.	No information on life cycle development	Cherif and Verheggen (2019)	Review	Belgium
	Chenopodium rubrum L.	No information on life cycle development	Cherif and Verheggen (2019)	Review	Belgium
	Spinacia oleracea L.	No information on life cycle development	EPPO (2024)	Database	
			Cherif and Verheggen (2019)	Review	Belgium
Cucurbitaceae	*Citrullus lanatus* (Thunberg) Mansfeld	No information on life cycle development	Cherif and Verheggen (2019)	Review	Belgium
	Cucurbita pepo L.	Oviposition observed; no completion of the life cycle	Ingegno et al. (2017a)	Greenhouse experiment	Italy
			Ingegno et al. (2017b)	Greenhouse experiment	Italy
			Cherif and Verheggen (2019)	Review	Belgium
Convolvulaceae	*Calystegia sepium* (L.) Robert Brown	No oviposition observed	Bawin et al. (2015)	Lab experiment	Belgium
			Cherif and Verheggen (2019)	Review	Belgium
	Convolvulus arvensis L.	No oviposition observed	Portakaldali et al. (2017)	Field experiment	Turkey
			Bawin et al. (2016)	Greenhouse and lab experiments	Belgium
			Cherif and Verheggen (2019)	Review	Belgium
Fabaceae	*Medicago sativa* L.	No information on life cycle development	EPPO (2024)	Database	
			Cherif and Verheggen (2019)	Review	Belgium
	Phaseolus vulgaris L.	Oviposition observed; no completion of the life cycle	Idriss et al. (2020)	Lab and field experiments	Sudan
			Cherif and Verheggen (2019)	Review	Belgium

Table 2. Continued.

Family	Species	Life Cycle Information	Reference	Study type	Study Location
			Ingegno et al. (2017a)	Greenhouse experiment	Italy
			Ingegno et al. (2017b)	Greenhouse experiment	Italy
			EPPO (2024)	Database	
	Vicia faba L.	Partial life cycle observed	Abdul-Ridha et al. (2012)	Field experiment	Iraq
			Cherif and Verheggen (2019)	Review	Belgium
			Bawin et al. (2016)	Greenhouse and lab experiments	Belgium
			Ingegno et al. (2017a)	Greenhouse experiment	Italy
			Ingegno et al. (2017b)	Greenhouse experiment	Italy
Euphorbiaceae	*Jatropha curcas* L.	No information on life cycle development	EPPO (2024)	Database	
			Cherif and Verheggen (2019)	Review	Belgium
Geraniaceae	*Geranium robertianum* L.	Oviposition observed; no completion of the life cycle	Ingegno et al. (2017a)	Greenhouse experiment	Italy
			Ingegno et al. (2017b)	Greenhouse experiment	Italy
			Cherif and Verheggen (2019)	Review	Belgium
Malvaceae	*Malva sylvestris* L.	Partial life cycle observed	Cherif and Verheggen (2019)	Review	Belgium
			Bawin et al. (2016)	Greenhouse and lab experiments	Belgium
Asteraceae	*Sonchus oleraceus* L.	No information on life cycle development	Tarusikirwa et al. (2020)	Review	Botswana
	Xanthium brasilicum Vellozo	No information on life cycle development	Cherif and Verheggen (2019)	Review	Belgium
	Xanthium strumarium L.	No information on life cycle development	EPPO (2024)	Database	
			Cherif and Verheggen (2019)	Review	Belgium
			Pandey et al. (2023)	Review	Nepal
Poaceae	*Sorghum halepense* (L.) Persoon	No information on life cycle development	Xian et al. (2017)	Review	China

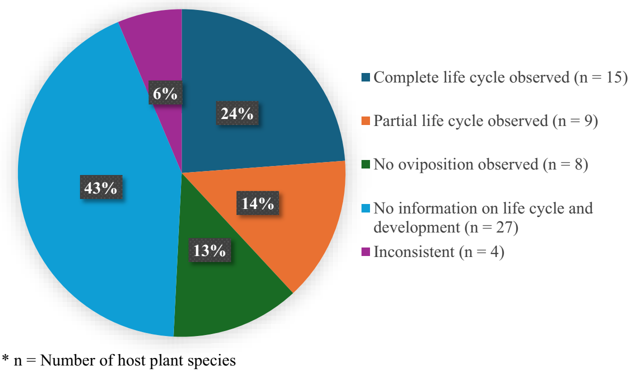

Fig. 1. Life cycle and development of *Phthorimaea absoluta* on 63 host plant species, based on published data.

closely associated with the nutritional quality of host plants (Bernays 2001, Galdino et al. 2011) and the variability in volatile organic compound profiles among potential host plants (Cherif and Verheggen 2019, Proffit et al. 2011). Female oviposition behavior also is shaped by prior experiences (Cherif and Verheggen 2019, Sawadogo et al. 2022), larval experiences (Caparros Megido et al. 2014), levels of host plant infestation and parasitism (Bawin et al. 2014), and complex interactions with conspecifics (Bawin et al. 2014, Sawadogo et al. 2022). Study results have also highlighted the role of trichomes in determining suitable oviposition sites, supporting the importance of trichomes in host plant selection (Chen et al. 2018, Khederi et al. 2014, Mirhosseini et al. 2022, Oriani and Vendramim 2010). Factors such as flight behavior, olfactory detection capabilities, and site

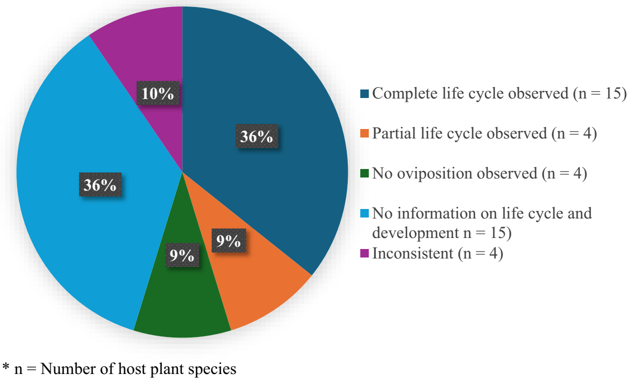

Fig. 2. Life cycle and development of *Phthorimaea absoluta* on 42 host plant species of the family Solanaceae, based on published data.

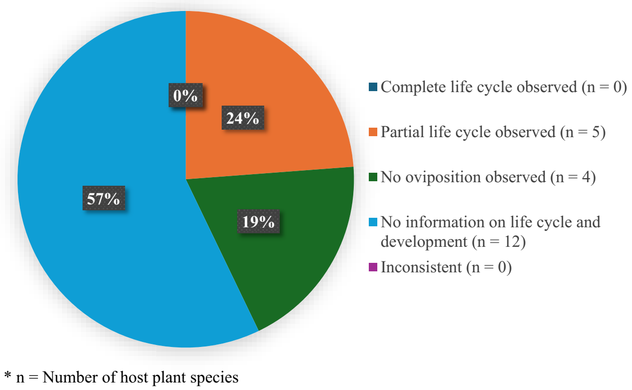

Fig. 3. Life cycle and development of *Phthorimaea absoluta* on 21 host plant species of non-Solanaceae, based on published data.

coloration also significantly influence the host plant preferences of female *P. absoluta* (Uzun et al. 2015).

Host plant preferences of the larval stage. First-instar *P. absoluta* typically remain at the oviposition site because of their limited mobility and the initially high nutritional value of the leaves on which eggs are deposited (Galdino et al. 2015). As these leaves age and their nutritional quality deteriorates, a process potentially accelerated by the feeding activity of *P. absoluta,* third instars migrate to apical leaves, which provide superior nutrition (Galdino et al. 2011, Hoy et al. 1998, Lim et al. 2007). This behavioral adaptation enhances feeding efficiency and supports optimal larval development. By advancing through developmental stages more rapidly, these larvae minimize their exposure to natural predators and adverse biotic and abiotic factors, thereby reducing mortality risks (Cornelissen and Stiling

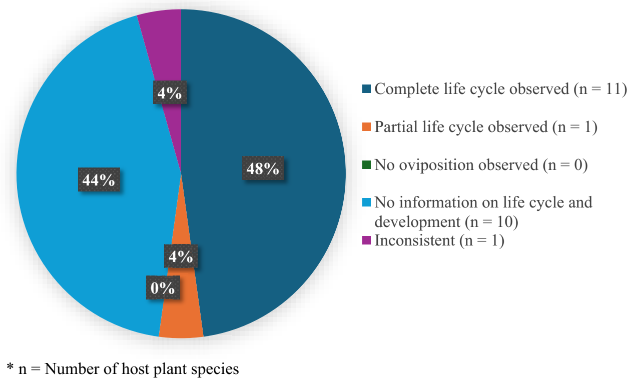

Fig. 4. Life cycle and development of *Phthorimaea absoluta* on 23 host plant species of the genus *Solanum,* based on published data.

2006, Galdino et al. 2015, Scriber 2002). Rarely do species exhibit both optimal oviposition site selection by females and effective feeding site selection by larvae. Typically, when larvae demonstrate the ability to select high-quality food sources, females may lack this precision and vice versa (Galdino et al. 2015, Li and Liu 2015, Thompson 1988). The choice of the oviposition site by females does not always guarantee suitability for larval development, because females may occasionally select suboptimal hosts (Bernays and Chapman 2007). This discrepancy can arise from various factors. In some cases, females may reject an otherwise suitable host plant because of intraspecific variation in plant chemistry or other traits (Bernays and Chapman 2007). The decision-making process underlying host selection is often guided by chemical concentrations, which may not consistently align with the plant's suitability for larval growth (Bernays and Chapman 2007). Opportunistic colonization, where females oviposit on a plant merely because of its availability, can also result in suboptimal host choices (Bawin et al. 2016).

Mismatch between female *P. absoluta* oviposition preference and larval development. In our literature review, we identified 63 host plant species utilized by *P. absoluta* females for oviposition. These host plants were evaluated for their suitability for supporting the pest's complete life cycle, incorporating both oviposition preferences and larval development (Fig. 1; Table 2). Our analysis revealed that 24% of these host plant species, which provide optimal conditions for the complete development of *P. absoluta,* belong exclusively to the Solanaceae. This finding underscores the critical role of Solanaceae in defining the pest's host range (Fig. 1; Table 2). Key Solanaceae hosts include *Atropa belladonna* L., *Lycium halimifolium* Miller, *Nicotiana glauca* Graham, *Nicotiana rustica* L., *Solanum aculeatissimum* Jacquin, *Solanum aethiopicum* L., *Solanum americanum* Miller, *Solanum dulcamara* L., *Solanum gilo* Raddi, *Solanum habrochaites* S. Knapp & D.M. Spooner, *S. lycopersicum, Solanum tuberosum* L., *Solanum muricatum* Aiton, *Solanum nigrum* L., and *Solanum sarrachoides* Sendtner. Partial development of the *P. absoluta* life cycle was observed on host plants from other families, including Cucurbitaceae, Fabaceae, Geraniaceae, and Malvaceae, which indicates that although some Solanaceae species can fully support the pest's development, not all members of this family are equally suitable (Fig. 2).

Discrepancies in earlier studies regarding host suitability likely stem from mismatches between female *P. absoluta* oviposition preferences and larval developmental success. For example, Bawin et al. (2015) reported that *Datura stramonium* L. supported the complete development of *P. absoluta*. However, Arnó et al. (2019) observed oviposition on *D. stramonium* without subsequent larval development, and other researchers have deemed this plant unsuitable for either oviposition or larval growth (Abbes et al. 2016, Smith et al. 2018). Although Bawin et al. (2016) documented only partial larval development on *Nicotiana tabacum* L., in subsequent studies (Aslan and Birgücü 2022, Jiang et al. 2023) *P. absoluta* completed its life cycle on this host. In contrast, *Solanum melongena* L. has been consistently recognized as a suitable host supporting the complete life cycle of *P. absoluta* except in the study by Idriss et al. (2020). These authors, based on field observations, collected only 133 of 10,954 larvae from all host plants, leading the authors to classify *S. melongena* as suboptimal for pest development. However, other research has consistently supported classification of this plant as an optimal host (Table 2).

Our analysis revealed that Solanaceae species were the only host plants supporting the optimal development of *P. absoluta* (Figs. 2, 3). According to Sylla et al. (2019), the suitability of a host plant for *P. absoluta* development is determined by larval survival rates and development time. For example, these authors classified *Capsicum annuum* L. and *Capsicum frutescens* L. as unsuitable hosts because of low survival rates and prolonged development time. Although *Capsicum chinense* Jacquin and *Solanum paniculatum* L. (Silva et al. 2021) and *Withania somnifera* L. (Subramani et al. 2021) were deemed suitable for oviposition, there is no conclusive evidence supporting their suitability for optimal larval development (Table 2). Non-Solanaceae species, such as *Cucurbita pepo* L., *Phaseolus vulgaris* L., *Vicia faba* L., *Geranium robertianum* L., and *Malva sylvestris* L., were also selected as oviposition hosts but failed to support optimal larval development (Table 2). These findings challenge the preference–performance hypothesis (Clark et al. 2011, Gripenberg et al. 2010, Menacer et al. 2021), which suggests that the oviposition preferences of *P. absoluta* females should align with conditions favorable for larval development and successful life cycle completion. Geographical variation across studies further highlights the complexity of this relationship. Female preferences and larval performance on the same host plant species often yield differing bioassay results depending on the region (Table 2). This variation may reflect ongoing differentiation in preference traits within *P. absoluta* populations, contributing to the divergence of host ranges and inconsistencies in host plant preferences across locations (Sylla et al. 2019). Nutritional stress has also been identified as a key factor contributing to these inconsistencies. Jaumann and Snell-Rood (2019) found that nutritional stress experienced during adulthood reduces investment in reproductive traits, including behavioral aspects, whereas stress during the larval stage increases investment in flight capacity, likely to enhance dispersal from nutrient-deficient environments. Friberg et al. (2015) further found that the relationship between female host selection and offspring success is not stronger in specialist herbivores than in generalists. They noted that specialists often underperform on their preferred host plants relative to generalists. This observation supports the notion that preference and performance traits in *P. absoluta* evolved largely independently, contributing to the preference–performance mismatch.

Salazar-Mendoza et al. (2023) found that reduced morphological and chemical defenses, lower constitutive volatile emissions, and decreased leaf nutritional quality significantly reduced oviposition rates, even on host plants suitable for larval development. Conversely, when herbivorous insects restrict themselves to a narrow host range, such as a single host plant species, the preference–performance relationship becomes more predictable (Dervisoglou et al. 2022). However, the broad host range of *P. absoluta* complicates this dynamic. Natural enemies also play a pivotal role in shaping host plant preferences of *P. absoluta*. For instance, Dervisoglou et al. (2022) found that high egg densities attract multiple egg predators, which suppress oviposition. Ingegno et al. (2013) found that *Dicyphus errans* (Wolff), a predator targeting eggs and first instar larvae, shares several host plants with *P. absoluta,* such as *S. tuberosum, Datura* spp., *Nicotiana* spp., *S. nigrum,* and *S. melongena*. Predation pressure from such predators likely influences host avoidance behavior, further complicating the preference–performance relationship.

Genetic studies on *P. absoluta* have indicated significant global homogeneity in genetic diversity (Cifuentes et al. 2011, Guillemaud et al. 2015, Ndiaye et al. 2021, Shashank et al. 2018, Shinthiya and Natarajan 2019, Wang et al. 2023). However, local conditions may drive genetic variability, influencing host plant preferences. The complex mosaic of genotypes within *P. absoluta* populations can result in a female shifting toward novel host plants while retaining a preference for the primary host, tomato. Genetic factors, including loci on the Y chromosome, may further contribute to the mismatch between female oviposition preferences and larval developmental success (Bernays and Chapman 2007). When nonecological barriers to gene flow are minimal, these traits can evolve rapidly, potentially leading to reproductive isolation (Forister 2004). Collectively, these findings underscore the intricate interplay of environmental, genetic, and ecological factors driving the observed mismatch between female oviposition preferences and larval developmental success in *P. absoluta*. These dynamics highlight the need for further research to disentangle the relative contributions of these factors to the pest's host plant utilization.

Variability of host plant preferences of *P. absoluta* within the same host plant genus. Survey results revealed significant variation in the host plant preferences of *P. absoluta,* even among species within the same genus (Table 2). Within the genus *Capsicum,* the pest's preferences generally followed a consistent pattern, with the notable exception of *C. annuum*. Although some researchers have reported *C. annuum* as rejected by female moths for oviposition, others have obtained contrasting results (Osman et al. 2021, Smith et al. 2018). For the genus *Datura, P. absoluta* was able to complete its life cycle on *D. stramonium* according to Bawin et al. (2015), whereas Arnó et al. (2019) observed only partial development. Several authors have classified *D. stramonium* as an unsuitable host because of the absence of oviposition (Abbes et al. 2016, Smith et al. 2018). Other species within the genus, such as *Datura ferox* L., were consistently avoided by female moths in multiple bioassays (Abbes et al. 2016, Galarza 1984). For *Datura quercifolia* Kunth, information remains insufficient to determine its suitability as a host plant (Pandey et al. 2023, Tarusikirwa et al. 2020). Within the genus *Nicotiana, P. absoluta* successfully developed on *N. glauca* and *N. rustica* (Table 2). However, *N. tabacum* was identified as only partially suitable for larval development by Bawin et al. (2016), although it was frequently cited as a primary host in several reviews and other studies (Aslan and Birgücü 2022, Jiang et al. 2023, Pandey et al. 2023). The most pronounced variabilities in host plant preferences were observed within the genus *Solanum* (Fig. 4), the largest genus in the Solanaceae (Hilgenhof et al. 2023). These variations highlight the complexity of host plant selection and suggest that factors such as local environmental conditions, plant chemistry, and genetic diversity within *P. absoluta* populations may contribute to these discrepancies.

We identified 23 *P. absoluta* host plant species within the genus *Solanum* through our literature review. Of these, 48% supported the complete life cycle development of *P. absoluta* (Fig. 4). Although in the majority of studies, excluding that by Idriss et al. (2020), *S. melongena* was identified as a suitable host supporting the pest's full life cycle, the controversy regarding the status of this plant as an ideal host persists. Variabilities in the host suitability of non-Solanaceae species remain challenging to address because of insufficient information on the ability of these species to support completion of the pest's life cycle (Table 2). Specialist phytophagous insects such as *P. absoluta* often undergo host shifts toward plant species that are morphologically, chemically, and taxonomically related to their primary hosts, thereby expanding their host range (Dalin et al. 2006, Sylla et al. 2019). Phylogenetic distance has been identified as a critical factor influencing female oviposition preferences (Nylin et al. 2014). However, in some studies phylogeny alone did not fully account for invasive traits; host plant–pest interactions frequently do not align perfectly with phylogenetic relationships. This misalignment has resulted in notable variations in host range and feeding patterns (Buonaiuto et al. 2023, Gaston et al. 1992, Gougherty and Davies 2021). Researchers have suggested that the phenological stages of host plants may significantly influence the oviposition preferences of lepidopteran female moths (Forister 2005, Smyth et al. 2003). Phenological differences among species within the same genus could lead to variations in host plant preferences. Hierarchical oviposition preference, wherein female moths exhibit a ranked preference for specific host plants, also may contribute to differences in host selection, even within the same genus (Smyth et al. 2003). The natal habitat preference induction hypothesis posits that female herbivorous insects tend to lay eggs on the same plant species on which they developed as larvae (Moreau et al. 2008, Salgado and Saastamoinen 2019). However, shifts to other host plants may occur when preferred hosts are unavailable (Sylla et al. 2019) or as part of a "spread-the-risk" strategy, in which females distribute their eggs across multiple host plants to mitigate predation risks (Berger et al. 2012, Bernays and Chapman 2007, Mochioka et al. 2021).

These factors collectively help explain the variabilities observed in the host plant preferences of *P. absoluta,* even among closely related species within the same genus. An understanding of these dynamics is crucial for accurately predicting the pest's host range and devising targeted management strategies. Precise host plant identification is also critical for polyphagous herbivorous insects; inaccurate records can lead to misinterpretations of their ecology and invasion potential. Polyphagous pests in particular have varying host preferences shaped by environmental factors, influencing their population dynamics and agricultural impact. For example, as a highly polyphagous pest, *Spodoptera frugiperda* (fall armyworm) shows variation in host plant suitability, with maize the most suitable host, although larvae also feed on other crops such as wheat, soybean, tomato, and cotton to varying degrees. However, on Chinese cabbage, only 5.3% of larvae reached adulthood, suggesting that some plants are not ideal for full development despite being used for feeding (Wang et al. 2020). These findings underscore the importance of accurately documenting host suitability and distinguishing between larval feeding preferences and successful development even when evaluating host ranges of polyphagous herbivores. The framework introduced in the present study also can be used to improve host-use assessments by addressing inconsistencies between reported and actual larval development, and enhancement of host record accuracy contributes to more reliable pest risk assessments, better outbreak predictions, and stronger biosecurity measures for managing polyphagous insect pests.

Conclusion

The host plant interactions of *P. absoluta* reveal a complex ecological framework that challenges traditional perspectives on host selection and utilization by specialist herbivores. This review highlights notable mismatches between female oviposition preferences and larval developmental success, emphasizing the pivotal role of the factors in shaping the pest's host range and ecological adaptations. Although *P. absoluta* primarily specializes in Solanaceae, significant variabilities were observed even among closely related species within the same genera, such as *Solanum, Datura,* and *Nicotiana*. These variations likely reflect the influence of factors such as plant chemical composition, nutritional quality, and local ecological pressures, including interactions with natural enemies and environmental conditions. The observed mismatch between oviposition choices and conditions optimal for larval development underscores the independent evolution of preference–performance traits and demonstrates the pest's adaptive plasticity. Geographic variability further complicates host plant records, suggesting that local environmental and genetic factors significantly influence host suitability. The prevalence of incomplete life cycle development on many host plants and the large proportion of species for which data were insufficient underscore the need for standardized methodologies and comprehensive research to clarify host plant utilization. By elucidating the ecological mechanisms underlying these mismatches and variabilities, this review contributes to a more precise definition of the host range of *P. absoluta*. Its true host range is confined to a subset of Solanaceae species that fully support the pest's complete life cycle, confirming that *P. absoluta* is an oligophagous herbivorous insect. These findings provide critical insights into the broader ecological and evolutionary dynamics of host specialization and pest adaptations, offering a foundation for future investigations into the ecological underpinnings of invasive herbivorous pests.

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