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RESEARCH

Empoasca fabalis DeLong (Hemiptera: Cicadellidae) in European sweet potatoes: records, leaf damage, and Auchenorrhyncha insights

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Abstract The recent surge in sweet potato (*Ipomoea batatas*) cultivation in Europe prompted an investigation into associated entomofauna within Portugal's southwestern region, known for its long-standing sweet potato production. This study aimed to assess entomofauna associated with this culture.
Insect sampling was conducted by leaf and sweep net across three regional sites during 2018 and 2019 revealing the presence of *Empoasca fabalis*. Histological examination of sweet potato leaves affected by *E. fabalis* feeding unveiled significant damage, including the emergence of whitish spots (termed "stipples") and subsequent necrotic spots. Comparative analysis between infested and undamaged control leaves revealed significant damage, involving mesophyll cell content deprivation and cellular disruption. This study describes, for the first time, the histological nature of the necrotic damage and suggests that *E. fabalis* primarily acts as a stippler on sweet potatoes, mainly targeting mesophyll cells with limited consumption of vascular tissue. The invasive behaviour and wide host range of *E. fabalis* pose a threat to sweet potato cultivation. These findings emphasize the need for monitoring to address the potential impact of *E. fabalis* on Europe's agricultural ecosystem and native vegetation. In addition, six other Auchenorrhyncha species were identified during this study, including four crucial vectors of plant diseases: *Laodelphax striatellus*, *Psammotettix alienus*, *Anaceratagallia glabra*, *Austroagallia sinuata*, together with *Empoasca solani* and *E. alsiosa*. These results emphasise the importance of managing these insects in sweet potato cultivation.

Keywords Leafhopper · Cicadomorpha · *Ipomoea batatas* · Mesophyll-feeder · Salivary secretions · Feeding behaviour

Introduction

Sweet potato, *Ipomoea batatas* (L.) Lam., belongs to the Convolvulaceae family which comprises

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approximately 59 genera and 1550 species (Carlquist & Hanson, 1991). Within the Convolvulaceae, the *Ipomoea* genus is the largest, containing around 600–700 species, primarily originating from the Americas (Austin & Huáman, 1996). *Ipomoea batatas* was brought into Europe by Columbus at the end of the fifteenth century (Akoroda, 2009). Subsequently, sweet potato has become globally widespread, and thanks to Portuguese and Spanish navigators, is now cultivated in over 100 countries (Truong et al., 2018).

The cultivation of sweet potatoes has gained significant prominence in Europe, especially in southern countries like Portugal, Spain, Italy, France, and Greece (Sawicka et al., 2022). In recent years, there has been a substantial rise in sweet potato consumption, attributed to its well-documented health benefits. Renowned for its nutritional richness and low glycaemic index, sweet potatoes are recognized as a highly nutritious food source (Bovell-Benjamin, 2007; Kays, 2005). Furthermore, various medical properties have been attributed to different parts of the sweet potato plant (Kang et al., 2014).

In mainland Portugal, there has been noteworthy growth in sweet potato production and cultivated areas in recent years (Cruz et al., 2022). Approximately 80% of the mainland country's output is concentrated in the southern region, particularly within the irrigation perimeter of the Mira River. The regions of Aljezur and Odemira have a long tradition of sweet potato production (Lima et al., 2018). Notably, the locally renowned 'Lira' variety holds the European certification of "Protected Geographical Indication" (Official Journal of the European Union, 2008). However, crop productivity in the region faces significant challenges due to viral infections transmitted by whiteflies (Aleyrodidae) and aphids (Aphididae) (Boavida & Mateus, 2021). An entomological survey was conducted during the project PDR2020 -101–031922 (+BDMira) aimed to assess insect impact on sweet potato plots. Alongside aphids and whiteflies, the survey revealed the presence of several Auchenorrhyncha species, including *Empoasca fabalis* Delong (=*Empoasca batatae* Poos, 1933) (Hemiptera: Cicadellidae).

A recent review of the tribe Empoascini (Cicadellidae: Typhlocybinae) reported over 1300 valid species of *Empoasca*-like leafhoppers, and many among them are pests on economically important crops worldwide (Xu et al., 2021). These small, inconspicuous, green leafhoppers are best distinguished by their male genitalia. *Empoasca fabalis* has a widespread distribution across its native American continent, ranging from the southern United States to South America (Alam & Gibbs, 1984; DeLong, 1930; Langlitz, 1964; Squire, 1972; Wilson & Hilburn, 1991). Recent expansion has extended its range to Hawaii (Dietrich & Perreira, 2019). European records are from the Canary Islands (La Palma Island) (Lorenzo & Hermoso de Mendoza, 2000) and Madeira Island (Aguin-Pombo & Freitas, 2020). Like many Auchenorrhyncha, adult *E. fabalis* insert eggs into stems, petioles, and on the main rib of leaves (Cetraro & Ortiz, 1982) but also into secondary ribs (Cusipuma & Sanchez, 1992).

Empoasca fabalis exhibits an extensive host range, documented on 66 plant species across 30 different families in Madeira Island alone (Aguin-Pombo & Freitas, 2020). Notable hosts include economically significant crops like potatoes, velvet beans, jack beans, beans, lima beans, pigeon peas, pasture plants such as lucerne (alfalfa) and white clover, as well as ornamental plants, fruit trees and vegetable fibres (Aguin-Pombo & Freitas, 2020; Alam & Gibbs, 1984; Audant, 1932; Childers & Winters, 1947; DeLong, 1930; Langlitz, 1964; Puerto Rico Experiment Station, 1940; Ramírez-García et al., 1999; Smith & Barker, 1930; Wolcott, 1936). Though primarily associated with sweet potatoes, *E. fabalis* also feeds on potatoes and other *Ipomoea* species (*I. indica* and *I. purpurea*) (Paradell et al., 1990). In South America, *E. fabalis* is a pest for sweet potatoes (Cetraro & Ortíz, 1982; Cusipuma & Sanchez, 1992) but also causes substantial economic damage to crops such as pigeon peas (Alam & Gibbs, 1984) and common beans (Audant, 1932; Cetraro & Ortíz, 1982; Childers & Winters, 1947; DeLong, 1930; Paradell et al., 1990; Puerto Rico Experiment Station, 1940).

A high abundance of *E. fabalis* produces pronounced whitish spots (termed "stipples"), necrotic spots, and leaf curling (Poos, 1933), compromising photosynthesis and overall plant growth. Despite its recognized impact, the precise histological effects of this species on sweet potatoes, as well as its influence on tuber size, and yield remain unknown. Limited information exists regarding the anatomical impact of *Empoasca* spp. leafhoppers. Much of the information available comes from the already-studied feeding behaviour of the potato leafhopper, *E. fabae* (Harris, 1841), a North American model species (reviewed in Backus et al., 2005).

It is likely that all Typhlocybinae leafhoppers predominantly use the "cell rupture" feeding strategy as opposed to the salivary sheath feeding strategy of other leafhoppers (Backus et al., 2005). This means that *Empoasca* spp. rapidly probe/penetrate their "naked" stylets through multiple, parallel channels in host plant tissue in either a circular pattern or a planar arc, leaving behind only watery saliva or disconnected bits and pieces of gelling saliva, not a full salivary sheath (Backus et al., 2005). Feeding damage from *Empoasca* species can be strictly segregated into two types: 1) numerous whitish stipples on leaves due to a circular pattern of probing in mesophyll or 2) "hopperburn" consisting of large, usually marginal, yellow/chlorotic and necrotic regions of leaves accompanied by severe plant stunting and reduced reproduction, as shown for *Empoasca recurvata* (DeLong) on sweet potato (Fig. 1A; previously unpublished image provided by E.A. Backus). Different species are either "stipplers" or "burners" with no known overlap (Backus et al., 2005).

Hopperburn-initiating feeding by *E. fabae* exhibits significant variations between hosts, primarily attributed to variable performance of three diverse styles (today called "tactics") of stylet probing (Backus & Hunter, 1989; Backus et al., 2005). Rapid stylet movements in a planar arc cutting through meristematic vascular tissues in stems and large leaf veins, along with enzymatic watery saliva deposition, are implicated in causing "hopperburn," characterized by both mechanical and physiological effects that accumulate and spread over time (Ecale & Backus, 1995; Kabrick & Backus, 1990). Local feeding damage leads to phloem blockage and xylem reduction which, in turn, cause systemic effects and symptom development in areas far from the site of feeding (Backus et al., 2005). In contrast, observations indicate that during stippling by *Empoasca abrupta* (=*Hebata* (*Hebata*) *abrupta* (DeLong, 1931)) only the cells in or very near the path of the stylet's probing are affected, with no systemic effect from damaged vascular tissues (Backus et al., 2005; E.A.Backus, unpubl. data).

The objectives of this work are to document the occurrence of *E. fabalis* on the European mainland, analyse the damage it inflicts on sweet potato leaves using high-resolution histological examination, and explore the associations of Auchenorrhyncha species with sweet potatoes in Europe. This study provides insights for agricultural management in Portugal for this little-studied insect group in the Iberian Peninsula.

Material and methods

Study area and sampling plots

Insects were collected from three farms in Southwest Portugal (mainland) within sweet potato plots with the 'Lira' variety in 2018 and 2019 (Table 1, Fig. 2). Sampling in these two years was performed in different plots. Planting typically starts in April, with harvesting concluding in

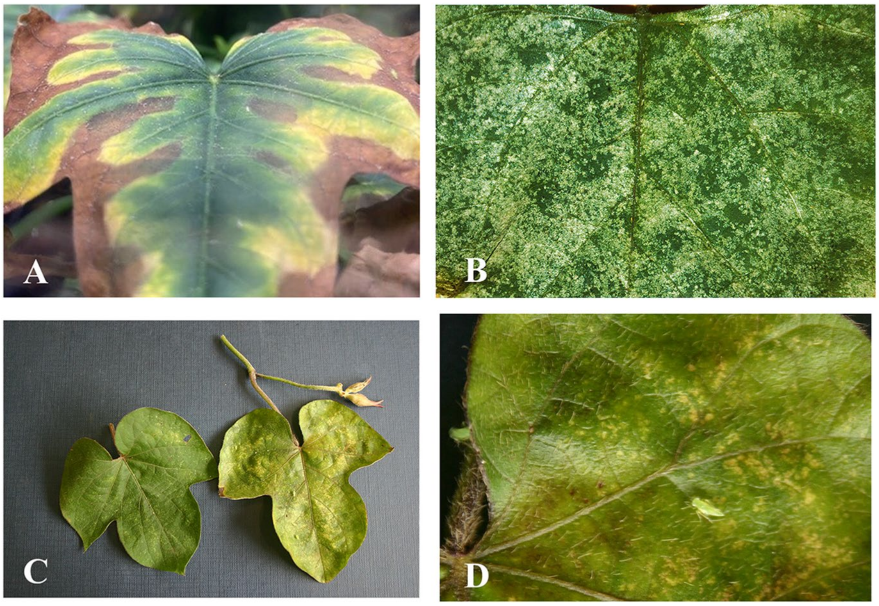

Fig. 1 Comparison of *Empoasca* spp. feeding symptoms. **A** – Hopperburn symptoms caused by *Empoasca recurvate* on sweet potato. **B –** Extreme leaf damage of palisade mesophyll cells caused by *Empoasca fabalis* feeding showing many, overlapping stipples leading to depigmentation and chlorotic spots. **C-** Undamaged sweet potato leaf (left) next to damaged left (right). **D** – Closeup view of *E. fabalis* nymph surrounded by many, individual stipples in leaf

November. Information regarding potential insecticide applications within these plots was not available.

Insect sampling

In mainland Portugal, two sampling methods, leaf and net sampling, were used monthly from July to September in 2018, and in July, October, and November in 2019. For leaf sampling, fifty sweet potato leaves were collected at random per plot at each sampling date. Sweep net sampling was performed over the crop plants, however, a standardized sweeping procedure (regarding the number and location of sweeps per plot and date) was not followed. Collected leaves were later examined in the laboratory under a stereoscopic microscope. Insects collected via vegetation sweeping were carefully removed from the net using a field aspirator and then killed with ethyl acetate. Both leaves and insects were transported to the laboratory in a cooler with freezer packs.

Table 1 Information on sweet potato plots surveyed in Southwest Portugal in 2018 and 2019

Farm	Location	Year	Area (ha)	Altitude (m)	GPS Coordinates
A	São Teotónio, Odemira, Beja	2018	0.48	84	37° 27′ 14.71’’N 8° 46′ 17.03’’W
		2019	1.36	64	37° 27′ 44.51’’N 8° 46′ 07.57’’W
B	Almograve/ Longueira, Odemira, Beja	2018	0.5	60	37° 36′ 32.94’’N 8° 47′ 58.43’’W
		2019	0.5	60	37° 36′ 38.21’’N 8° 47′ 56.05’’W
C	Odeceixe, Aljezur, Faro	2018	0.5	104	37° 24′ 24.64’’N 8° 46′ 34.21’’W
		2019	0.5	104	37° 24′ 25.00’’N 8° 46′ 34.00’’W

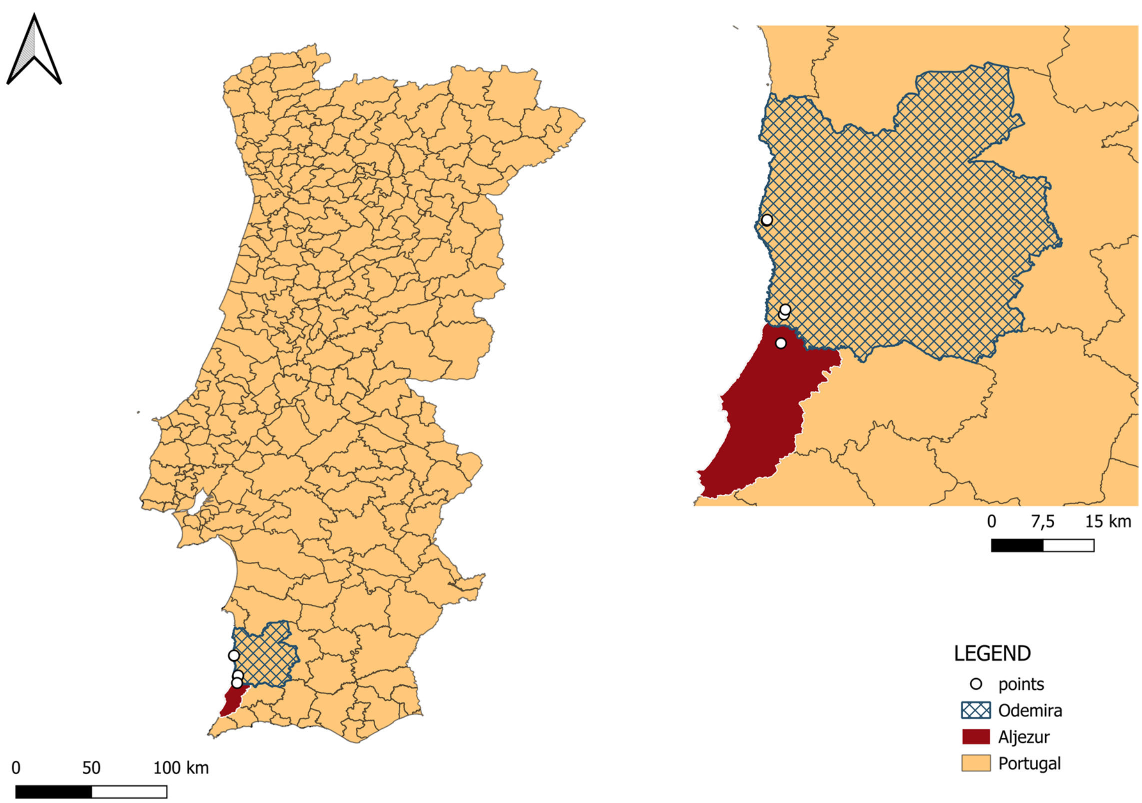

Fig. 2 Location of study areas in southern mainland Portugal

Insect identification

In the laboratory, the genital structures of the collected insects were dissected and boiled in a 10% KOH solution. Afterwards, they were rinsed in distilled water and mounted in glycerin. The identification of specimens except two that could not be conclusively identified was done according to Biedermann and Niedringhaus (2009), Della Giustina (1989, 2019), Dmitriev et al. (2023), and Ribaut (1936, 1952). Specimens were preserved and their genitalia were pinned beneath each specimen. Females lacking reliable identifying characteristics were assigned to voucher specimens deposited in the Entomology Collection of the University of Madeira (UMACI). A recent review of the tribe Empoascini transferred *E. fabalis* to a different genus, *Hebata* (*Hebata*) *fabalis* (DeLong, 1930), however, since previous literature refers to *E. fabalis* and this is an important economic species, we keep this name throughout the text (Xu et al., 2021).

Histological leaf damage assessment

To assess the anatomical damage caused by *E. fabalis* on sweet potato plants, histological sections from undamaged and heavily damaged leaves were compared. Samples of damaged leaves were collected in Madeira Island (Caniço, Santa Cruz) at the end of the growing season from a parcel in a heavily infested plantation, with *E. fabalis*, in an agricultural setting. The crop remained in the field for approximately one year, and over this period, the damage consistently increased over time (Aguin-Pombo, pers. obs.).

For histological assessment, control and symptomatic leaves of *Ipomoea batatas* were examined under a stereomicroscope (Leica MZ8). Images were captured using NIS Elements Software V1.10.00 (Nikon Instruments, Melville NY, USA). One square centimeter blocks were collected from five undamaged leaves (Fig. 3A) and five *E. fabalis*-damaged leaves exhibiting chlorotic and necrotic spots (Fig. 3B).

To identify evidence of feeding activities, leaf samples were fixed in a formaldehyde–acetic acid–alcohol solution with proportions 1:1:18 (38% formaldehyde: glacial acetic acid: 70%: ethanol) for 48 h at room temperature. Subsequently, they underwent dehydration through a standard ethanol series, followed by embedding in paraffin and serial-sectioning at 10 µm using a Leica RM 2255 microtome. Sections were stained with Astra blue + safranin, and cover slipped with Entellan®. Cross sections of the leaves were examined at a light microscope (Leica, DM 2500 LED) to identify salivary deposits (red staining) and anatomical damages. Images were acquired using Leica Application Suite X 5.1.0.25446 software.

Results

1. Record of occurrence of *Empoasca fabalis* on the European mainland

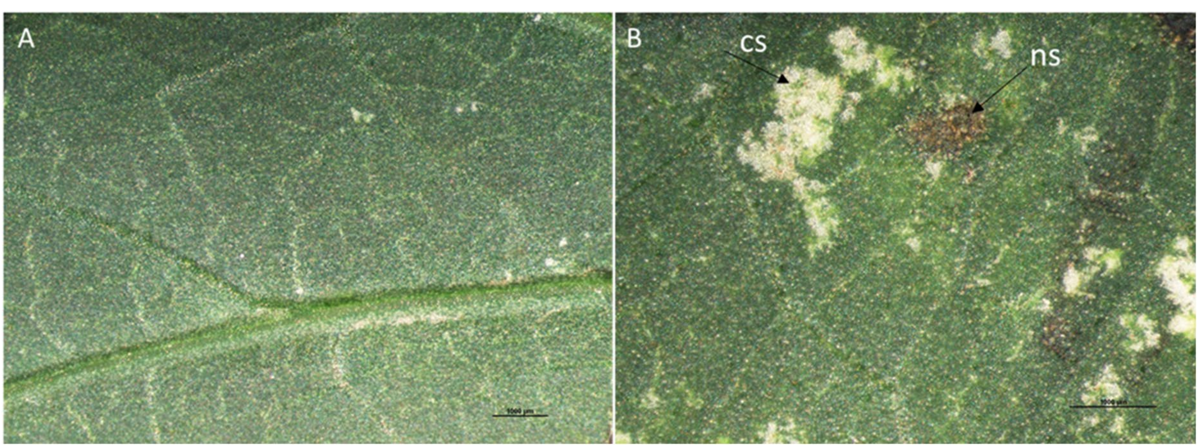

Fig. 3 Adaxial face of sweet potato leaf. **A**—Non syntomatic. **B** – Leaf damage of palisade mesophyll cells caused by *Empoasca fabalis* feeding showing depigmentation, chlorotic spots (cs), and necrotic spots (ns). Scale bar = 1000 µm

The populations of *E. fabalis* in sweet potato crops in mainland Portugal were low, and the overall infestation was not severe. We identified eight individuals of *E. fabalis* from two farms in Odemira (São Teotónio and Almograve) during October and November 2019 (Table 1, Supp. Info.). In contrast, nearly 99% of leafhoppers found in the sweet potato crops in plantations on Madeira Island were identified as *E. fabalis* (Aguin-Pombo & Freitas, 2020; unpublished data). Thus, on Madeira Island, *E. fabalis* is now the predominant species infesting sweet potatoes.

2. Leaf damage assessment

Observations in the present study show that *E. fabalis* performs similar stippling as *Empoasca abrupta* (Figs. 1B-D). However, population numbers of stippling *Empoasca* spp. can become so great that numerous stipples on leaves overlap and coalesce (Fig. 1B), causing leaf necrosis and collapse. Thus, when populations are high, it can be difficult to determine whether damage is due to stippling or hopperburning.

Appearance of control leaves

Histological analysis of control leaves exhibited typical anatomical characteristics: both upper and lower leaf surfaces had normal-looking epidermal cells with thick cell walls (Fig. 4A); adaxial and abaxial cells of the epidermis showed no irregularities; palisade cells exhibited a well-organized structure and contained abundant chloroplasts (Fig. 4B, C). These cells were arranged, with only a few discernible intercellular spaces between them. In the spongy parenchyma cells, intercellular spaces were more apparent and abundant, consistent with the typical structure of parenchymal leaves (Fig. 4B). There was no evidence of empty cells or indication of cell disruption. The vascular tissues appeared to be organized and complete (Fig. 4C).

Cellular abnormalities of damaged leaves

Macroscopic observations of damaged leaves revealed characteristic symptoms, including distinctive whitish-tan spots (termed stipples) and dark brown necrotic spots (Fig. 3B). Necrotic spots likely represent later progression of stipples from emptied cells to cell death, characterized by dark, dead tissue in the form of spots or lesions on the leaves (Fig. 3B).

Comparing histological sections between undamaged (Fig. 4) and damaged areas of leaves (Fig. 5) revealed distinct anatomical differences between the two types of damage. When comparing stippled (Fig. 5A) and necrotic (Fig. 5B) regions, a progression of damage is evident. Formation of stipples on the leaves indicate initial damage directly around sites of leafhopper stylet probing. Sections through stipples showed adaxial (upper) epidermal cells with irregularities and sunken areas where the cell contents were removed but cell walls were mostly intact (Fig. 5A). In the whitish region, palisade mesophyll cells displayed little cell wall damage, but showed removal of cell contents. Adjacent tissues remained relatively preserved (Fig. 5A). Cell content was removed in all directions around the probing site, creating a round, white stipple devoid of chloroplasts in a stereotypical area of 0.42 mm (Fig. 5B). After probing one site on the leaf, leafhoppers likely withdrew their stylets from the plant tissues and moved to another probing site (Fig. 5A). Red-staining deposits in the stipples (Fig. 5C) are localized in the tissues and close to small veins (Fig. 5D). The darkest stain in the mesophyll cells surrounding the phloem in Fig. 5D indicates the place of attack.

Sections through necrotic spots showed both the adaxial and abaxial epidermis with sunken areas and compressed cells (Fig. 5B). Palisade cells had larger intercellular spaces than were present in stipples, indicating spread of cell wall breakage. Necrotic spots corresponded to the presence of empty cells, distortion of cell organization, and extensive, bright, red-stained deposits, both in the palisade and spongy mesophyll tissues found in the same regions where cell disruption was evident (Fig. 5B-D). The deposits were numerous and visually distinguishable due to their bright red staining with safranin and distinct boundaries. They exhibited various forms, ranging from solid red to less dense, with a significant proportion of total deposits located more frequently in the palisade and spongy mesophyll but also nearby vascular bundles (Fig. 5B, C). Additionally, large deposits of calcium oxalate crystals were notably present in the upper cells of palisade parenchyma (Fig. 5B, C).

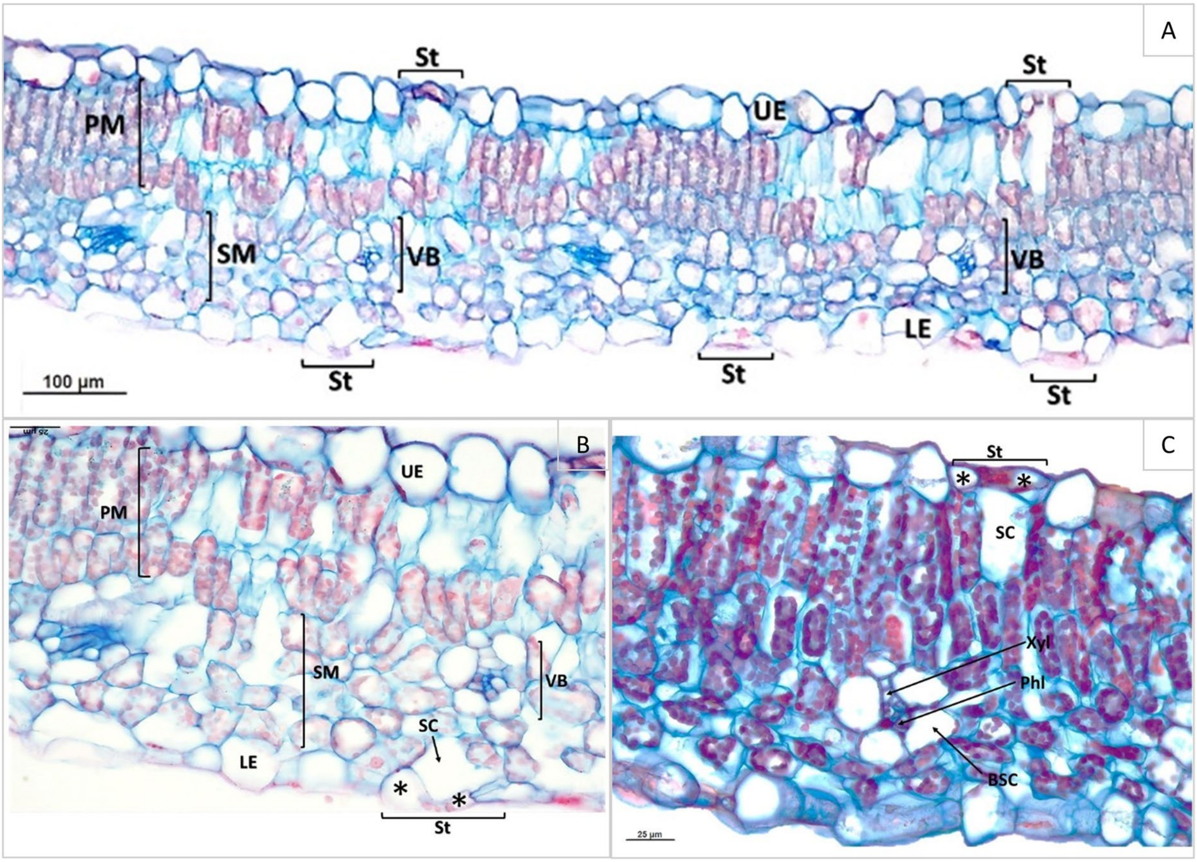

Fig. 4 Cross sections of a non-infested *Ipomoea batatas* leaf staining with Astra blue and safranin. **A**—Overview of a leaf section without damages. Scale bar = 100 µm; **B—**Details showing the leaf structure and especially the palisade mesophyll composed of one or two layers of elongated cells tightly compacted and rich in chloroplasts, and the spongy mesophyll composed of rounded cells, Scale bar = 25 µm; **C—**Normal vascular bundle, the cells are uniform in size and shape, Scale bar = 25 µm. BSC- Bundle Sheath Cell; LE- Lower Epidermis; Phl- Phloem; PM- Palisade Mesophyll; SC- Stomata Chamber; SM- Spongy Mesophyll; St-Stomata; UE- Upper Epidermis; VB- Vascular Bundle; Xyl- Xylem; and * St-Stomata Guard Cells

3. Associations of *Auchenorrhyncha* with sweet potatoes in Europe: distribution and host plants

Our investigation revealed thirty-two specimens, of which only twenty-nine could be identified (Table 2). All of them belonged to seven polyphagous Auchenorrhyncha species, all collected for the first time in sweet potatoes. These species include *Empoasca solani* (Curtis, 1846), *E. alsiosa* (Ribaut, 1933), *E. fabalis*, *Psammotettix alienus* (Dahlbom, 1850), *Anaceratagallia glabra* Dmitriev, 2020 (=*Agallia laevis* Ribaut, 1935), *Austroagallia sinuata* (Mulsant & Rey, 1855) and *Laodelphax striatellus* (Fallén, 1826) (Table 2).

Discussion

Empoasca fabalis in European mainland: a potential threat to European agriculture

Although Aguin-Pombo et al. (2014) briefly mentioned the presence of this species in the Iberian Peninsula, their report did not include specific location and field information. Therefore, the present study stands as the first officially documented record of *E. fabalis* in the European mainland and the first detection of this species in sweet potato in this region. Given the concentration of sweet

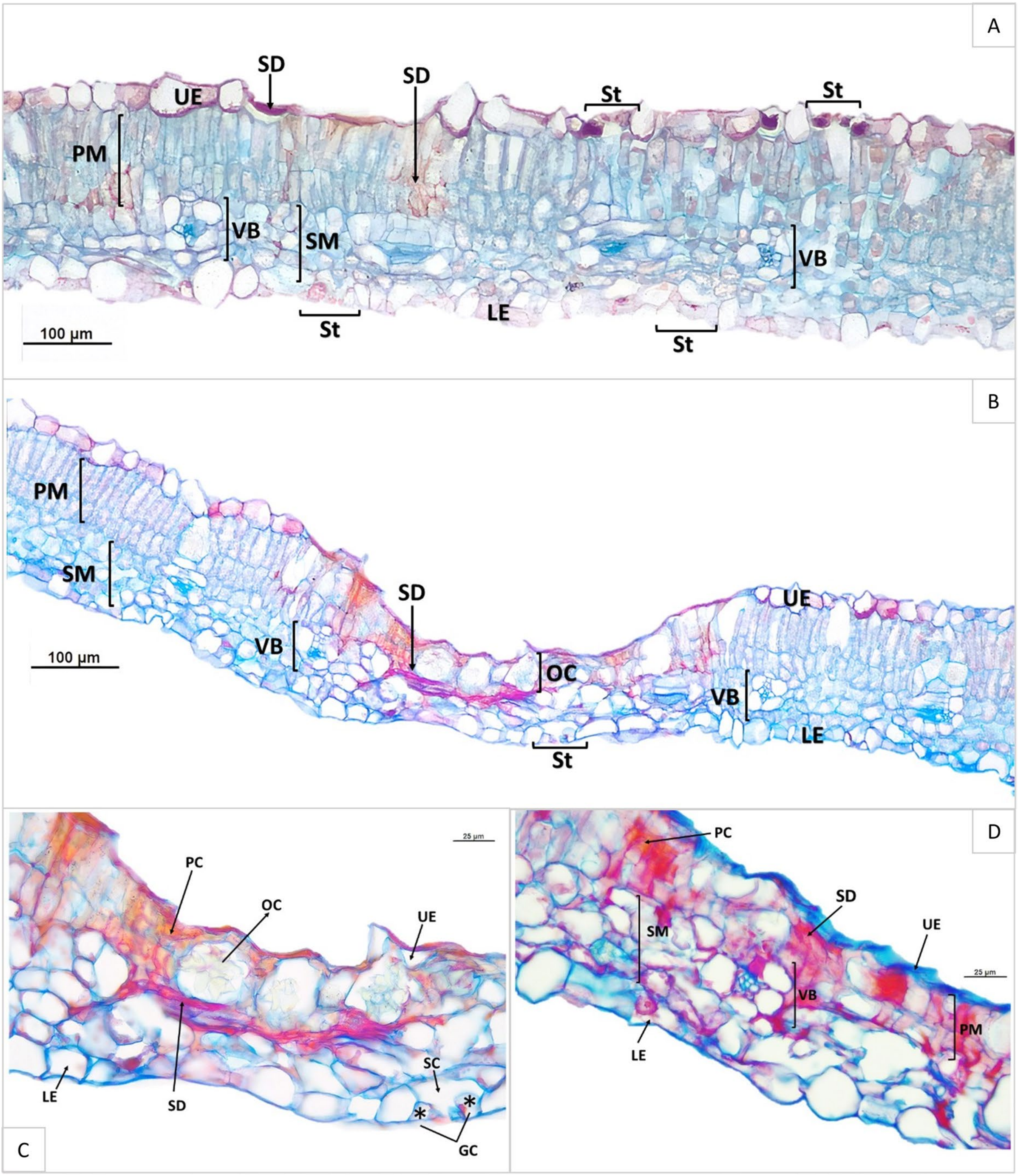

Fig. 5 Light micrographs of 10 µm transversal cross sections of *Ipomoea batatas* leaf exposed to feeding by *Empoasca fabalis*. **A—**Chlorotic region showing salivary deposits with minor cell damages (red, safranin staining) (SD), Scale bar = 100 µm; **B—**Necrotic region, Scale bar = 100 µm; **C** and **D—**Necrotic spot with physical disruption of vascular bundles and mesophyll tissues, Scale bar = 25 µm; GC- Guard Cells (*); LE- Lower Epidermis; OC- Calcium Oxalate crystals; PC- Phenolic Compounds; PM- Palisade Mesophyll; SC- Stomata Chamber; SD- Salivary deposits; SM- Spongy Mesophyll; St- Stomata; UE- Upper Epidermis; VD- Vascular Bundle

Table 2 Distribution and food/host plants of the species of Auchenorrhyncha collected during this study in sweet potato

Family	Species	Distribution		Food/Host plants
		World	**Iberian Peninsula**	
Delphacidae	*Laodelphax striatellus* (Fallén)	Worldwide, primarily temperate zones (Nast, 1972) and tropical regions across Asia (Philippines, some Indian and Pacific islands)	Widely distributed in the Iberian Peninsula (eg. Lallemand, 1928; Lindberg, 1960; Llácer et al., 1986; Medina, et al., 1981; Seabra, 1939)	Predominantly adventive plants
Cicadellidae	*Anaceratagallia glabra* Dmitriev	Western Palaearctic region up to Kazakhstan (Nast, 1972, 1987). In Europe, in central and Mediterranean countries	Widely distributed in the Iberian Peninsula (eg. Cardoso, 1974; Llácer et al., 1986; Lindberg, 1960; Medina et al., 1981)	Grasses and adventive plants
	Austroagallia sinuata (Mulsant & Rey)	Western Palaearctic, up to Kazakhstan (Nast, 1972, 1987). In Europe, in central Europe and Mediterranean countries	Present in Spain (eg. Llácer et al., 1986, 1988). In Portugal, there are only a few records from central and Southern Portugal (Alentejo) (Lindberg, 1960, 1962; Popova, 2020)	Predominantly on grasses and adventive plants
	Psammotettix alienus (Dahlbom)	Palearctic region (Nast, 1972, 1987). It is also in North and South Africa, Canada, the United States, and Australia	Present in Portugal and Spain (eg. Bolívar & Chicote, 1879; Cardoso, 1974; Lallemand, 1928; Lindberg, 1960; Seabra, 1939)	Cereal crops, adventive plants and grapevines (Bosco et al., 1997)
	Empoasca alsiosa Ribaut[a]	Mediterranean countries (Nast, 1972, 1987)	South Portugal, Southeast Spain, the Canary Islands, and the Madeira archipelago (eg. Cardoso, 1974; Chicau et al., 2009; Hermoso de Mendoza & Medina, 1979; Medina et al., 1981, 1982; Quartau et al., 1997)	Dicotyledonous grasses, shrubs, and trees (Cardoso, 1974; Mazzoni, 2005). Pest of citrus crops in Spain (Cabello & Pascual, 2006)
	Empoasca solani (Curtis)	Western Palearctic region up to Mongolia, and North Africa (Nast, 1972, 1987)	Common in the Iberian Peninsula (eg. Hermoso de Mendoza & Medina, 1979; Lasso y Lacha, 1948; Lindberg, 1960; Rebelo, 1993)	Grasses (Günthart, 1974; Vidano & Arzone, 1976), trees (Abdul-Nour, 2005; Günthart, 1974) and occasionally grapevines (Alvarez, 2020; Mazzoni et al., 2001). Pest of potatoes. In Portugal, large populations detected in stone fruits (Barateiro et al., 2021)
	Empoasca fabalis DeLong	From Southern United States to South America (eg. Alam & Gibbs, 1984; DeLong, 1930; Langlitz, 1964; Squire, 1972; Wilson & Hilburn, 1991)	South Spain and Portugal (Aguin- Pombo al., 2014; this work)	Polyphagous. Potatoes, velvet beans, jack beans, beans, lima beans, pigeon pea, pasture plants (lucerne, white clover), vegetal fibres (jute, cotton), ornamental plants (morning glories) and fruit trees (papaya) (eg. Adam & Gibbs, 1984; Aguin-Pombo & Freitas, 2020; Audant, 1932; Childers & Winters, 1947; DeLong, 1930; Langlitz, 1964; Puerto Rico Experiment Station, 1940; Ramírez-García et al., 1999; Smith & Barker, 1930; Childers & Winters, 1947; Wolcott, 1936)

Cardoso (1974) previously reported *Empoasca fabae* in Portugal; however, this was a misidentification of *E. alsiosa*

[a]Taxonomic remarks

potato production in southern European regions and the growing interest in its cultivation in central Europe (Sawicka et al., 2022), *E. fabalis* presence in sweet potato raises concerns about its potential spread across Europe and the production losses it can inflict.

Empoasca fabalis has a short life cycle of 28 to 39 days and high fertility rate of up to 107 eggs per female (Cusipuma & Sanchez, 1992). This rapid population growth can lead to infestations, making it a serious threat to crops. In some American regions, this species can produce up to 11 generations per year (Cusipuma & Sanchez, 1992), with similar patterns in the Canary Islands (Lorenzo Fernández & Hermoso de Mendoza, 2001; Lorenzo Fernández, 2003). Southern Europe's climate is appropriate for its reproduction. In fact, *E. fabalis* can adapt to a wide range of environmental conditions, from subtropical to temperate regions. Its also shows remarkable tolerance to sub-zero temperatures (-3ºC) and has the ability to overwinter successfully (Decker & Maddox, 1967). This adaptability suggests that the species could establish itself even in northern European regions.

The polyphagous nature of *E. fabalis* means it can feed on a variety of plant species. This trait increases its potential impact on European agriculture and native vegetation. Sweet potatoes may act as a reservoir for *E. fabalis*, facilitating its spread beyond sweet potato fields across different European regions. A monitoring effort should be done across a broader geographic area throughout the year to comprehensively assess its distribution and potential impact in Europe.

Leaf damage assessment

The visible effects of *E. fabalis* infestation observed in field plantations become conspicuous in the later stages of the crop cycle, characterized by extensive whitish spots ("stipples") across most leaves. Our findings support that the feeding behaviour of *E. fabalis* on sweet potatoes leads to the depletion of palisade mesophyll cells, creating discernible, contiguous depigmented zones on leaves. These stipples form during stylet probing when the leafhopper pierces plant tissue and extracts cellular content. Histologically, the damaged leaves display signs consistent with the consumption of mesophyll cell contents, particularly in the upper palisade mesophyll cells, accompanied by bright red-staining deposits. This observation aligns with previous studies of leafhoppers in the subfamily Typhlocybinae (especially tribes Empoascini and Erythroneurini), indicating similar feeding patterns within related taxa (Pollard, 1968; Saguez et al., 2015; Serrano & Backus, 1998; Smith & Poos, 1931). Similar to *E. abrupta* (Backus et al., 2005) and *Zyginidia scutellaris* (Herrich-Schäffer, 1838) (Marion-Poll et al,. 1987), *E. fabalis* ingests from primarily mesophyll and vascular tissues of small veins on leaves.

Empoasca fabalis feeding damage progresses to necrotic symptoms, appearing as dark, dead tissue in the form of spots or lesions on the leaves or other plant parts. Necrosis represents an advanced stage of leaf damage, involving more profound anatomical changes, including vascular disruption. Mechanical damage, enzymatic action, and plant defence responses typically trigger necrosis, leading to the death of affected plant cells (Backus et al., 2005). The extent and severity of necrosis vary depending on factors such as leafhopper population density, sweet potato variety susceptibility, and environmental conditions. In some cases, necrotic tissue can become susceptible to secondary infections by pathogens, further compromising plant health.

Ramified red-stained deposits are likely composed of mixed saliva and crushed, necrotized plant tissues, a unique hallmark of *Empoasca* spp. probing (Backus et al., 2005). Such deposits from *E. fabalis*, similar to those observed in other *Empoasca* species, likely contain enzymes that facilitate the breakdown of plant cells during feeding (Ecale & Backus, 1995; Kabrick & Backus, 1990; Serrano & Backus, 1998). Although the palisade mesophyll (adaxial surface) was more damaged than the spongy mesophyll (abaxial, lower) surface, we have no evidence of the direction of insertion of stylets for the likely many probes made into our examined tissues. Probing directly into the palisade mesophyll from the adaxial surface is possible. Alternatively, the insect could have probed from the abaxial surface through the intercellular spaces in the spongy mesophyll, then salivated and ingested primarily in the palisade layer above. Thus, while our evidence cannot demonstrate from which side of the leaf probing was initiated, it does provide conclusive evidence of stylet probing activity by *E. fabalis*. In addition, our work conclusively shows that *E. fabalis* targets more leaf mesophyll than large vascular tissues of stem or leaf, and also shows that stipples can progress to form necrotic spots on leaves. These observations support that *E. fabalis* causes damage to sweet potato from stippling, probably not hopperburning.

The damage on leaves was studied only in an agricultural setting on Madeira Island. Here the populations of *E. fabalis* are very large. However, since the leaves were gathered directly from the field, the exact timing of the damage occurrence remains uncertain. The combined impact of numerous insects feeding at various intervals can trigger biochemical responses at distinct times and rates. Consequently, this can lead to the variable occurrences of whitish spots versus necrotic areas that we have seen. Additionally, given the high populations of *E. fabalis* in Madeira and the fact that the crop remained in the field for approximately one year, their stippling behaviour could result in extensive leaf consumption over such a long duration. Ultimately, extensive necrosis would result. This prolonged feeding might superficially resemble symptoms of hopperburn.

The extensive stippling and cellular disruption around feeding sites can limit effective photosynthesis, potentially impacting overall growth and health. Under high population pressures, stippling can lead to whole-leaf destruction. However, the exact impact on crop production requires further assessments and depends on the timing and severity of damage during different crop stages. If leaf damage occurs primarily towards the end of the crop cycle when the tubers have already developed, the impact may be relatively negligible. However, early-season damage by large numbers of leafhoppers could cause a more significant impact. Thus, ongoing monitoring and analysis of leafhopper feeding damage are crucial for mitigating potential damage to sweet potato crops. Accurately assessing these types of damage ultimately requires the use of techniques such as AC-DC electropenetrography (EPG) (Backus & Shih, 2020; Backus et al., 2019). The extent of observed damage on the plant remains noteworthy and justifies further investigation.

Association of Auchenorrhyncha with sweet potatoes in Europe

The Auchenorrhyncha species found on sweet potatoes in mainland Europe have received no attention in research. Most of the species reported in this study are common and widely distributed across the western Palaearctic region (*A. sinuata*, *A. glabra*, *E. solani*) or are commonly found in Mediterranean climates (*E. alsiosa*). Interestingly, two of these, *L. striatellus* and *P. alienus,* exhibited a broader distribution, even colonizing tropical regions. All these species have been documented already in other studies from both mainland Spain and Portugal, as indicated in Table 2.

Primarily associated with grasses, these Palaearctic species (Nast, 1972, 1987) have now been found for the first time in sweet potatoes. Many of them play significant roles as vectors of plant pathogens (Table 3). This discovery underscores the importance of further ecological and behavioural investigations related to sweet potatoes.

Notably, all these species except for *Empoasca* possess the ability to transmit almost 20 disease agents to plants, such as viruses and phytoplasmas (Table 3). For instance, *A. glabra*, *A. sinuata*, *P. alienus* and *L. striatellus* act as vectors for the '*Candidatus* Phytoplasma solani' (Duduk et al., 2008), causing Bois noir, the most significant grapevine yellows in Europe and Mediterranean regions (Conigliaro et al., 2018). Additionally, species of *Austroagallia* have tested positive for aster yellows (Kruger et al., 2011). In the case of *E. fabalis*, it is believed that it may transmit plant pathogens, including the causal agent of the Papaya Bunchy Top Disease (Pantoja et al., 2002; Ramirez, 1997).

Considering that sweet potatoes can serve as a reservoir for these insect species, this crop may play a significant role in maintaining leafhopper populations throughout the year, potentially aiding in the spread of viral diseases. Therefore, there is a crucial need for deeper understanding of the Auchenorrhyncha fauna associated with sweet potatoes to better manage potential disease vectors and safeguard crop health. Studies on the population dynamics of *E. fabalis* in sweet potatoes, along with EPG monitoring of feeding damage, would clarify the impact

Table 3 Plant pathogens transmitted by the leafhopper and planthopper species collected in sweat potatoes during this study

Species	Pathogens of plant diseases	References
Laodelphax striatellus (Fallén)	Barley yellow striate mosaic cytorhabdovirus	Nahdi et al. (2020)
	Maize rough dwarf fijivirus	Vidano (1970)
	Northern cereal mosaic virus	Nahdi et al. (2020)
	Rice black-streaked dwarf fijivirus	Nahdi et al. (2020)
	Rice stripe tenuivirus	Nahdi et al. (2020); Zhang et al (2007)
	Maize Iranian mosaic virus	Nahdi et al. (2020)
	16SrI C phytoplasmas	Orságová et al. (2011)
	16SrI F phytoplasmas	Orságová et al. (2011)
	'*Candidatus* Phytoplasma solani'	Quaglino et al. (2019)
Anaceratagallia glabra Dmitriev	Eggplant mottled dwarf virus	De Stradis et al. (2008)
	16SrI phytoplasmas	Lavina et al. (2006)
	16SrIII-B phytoplasmas	Lavina et al. (2006)
	16SrXII-A phytoplasmas	Mirzaie et al. (2007)
	'*Candidatus* Phytoplasma solani'	Conigliaro et al. (2018)
Austroagallia sinuata (Mulsant & Rey)	16SrXII-A phytoplasmas	Carraro et al. (2008)
	16SrV phytoplasmas	Weintraub and Orenstein (2004)
	16SrI phytoplasmas	Sabate et al. (2003)
	16SrII phytoplasmas	Nahdi et al. (2020)
	'*Candidatus* Phytoplasma solani'	Quaglino et al. (2019)
Psammotettix alienus (Dahlbom)	Wheat dwarf virus	Nahdi et al. (2020)
	Russian mosaic virus	Wang et al. (2019)
	Wheat yellow striate virus	Nahdi et al. (2020)
	Oat dwarf viruses	Nahdi et al. (2020)
	Alfalfa leaf curl virus	Nahdi et al. (2020)
	16SrXII-A phytoplasmas	Drobnjaković et al. (2010)
	Psammotettix alienus reovirus (PARV)	Fu et al. (2020)
	'*Candidatus* Phytoplasma solani'	Quaglino et al. (2019)
Empoasca alsiosa Ribaut	Unknown	
Empoasca solani (Curtis)	Unknown	
Empoasca fabalis DeLong	Associated with Papaya Bunchy Top Disease	Ramirez (1997)

of this leafhopper species on sweet potato plants in crops in the European mainland and aid in the development of resistant varieties of sweet potato.

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Authors' contribution Conceptualization: DAP, CM; Field sampling and lab insect screening—CB, CM; Insect species identification- DAP; Manuscript writing- DAP, TV, CT, EB, CM; Histological procedures and figures- TV, CT; Other figures- DAP, EB; Tables-DAP, CM.

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Declarations

Competing interests The authors declare no competing interests.

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