



Maladaptive host choice by an alien leaf miner *Phyllonorycter leucographella* (Lepidoptera: Gracillariidae) has the potential to limit its invasiveness

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Abstract. Alien phytophagous insects are often introduced along with their host plants, creating opportunities for troublesome invasions. Yet, not all of them are able to successfully colonize novel host plants. In this study, we investigated host selection by the alien leaf miner *Phyllonorycter leucographella* (Zeller, 1850) on both its original host and novel host plants in the insect's alien range. We predicted that this insect's percentage infestation of the original host would be positively related to its specific leaf area (SLA), because high-SLA leaves are nutritious and have thin cuticles, traits related to high offspring developmental success. We further hypothesized that this host selection process would apply in the selection of novel host plants. Our results show that this leaf miner selects leaves of its original host plant, *Pyracantha coccinea*, according to their SLA values. The SLA value was also positively related to the probability of *P. leucographella* infesting and successfully developing on novel host plants. The selection of high-SLA plants by the moth leads to a high developmental success on novel host plants in the first (summer) generation, but it is likely to be maladaptive in the second (overwintering) generation, because in temperate Europe, high SLA values are associated with deciduous plants that shed their leaves in autumn. It is likely that the apparent maladaptive selection of novel host plants by *P. leucographella* reduces the invasiveness of this pest by preventing its establishment on native plants.

INTRODUCTION

Transportation and international trade are two of the main drivers of the spread of alien species (Levine & D'Antonio, 2003; Hulme, 2009; Lenda et al., 2014). Use of exotic plants in horticulture and urban greenery are particularly dangerous for native ecosystems, because alien phytophagous insects are often introduced along with their host plants, creating opportunities for troublesome invasions (Rabitsch, 2010). In fact, ornamental horticulture is the most important pathway for introducing alien arthropods to Europe, contributing to as much as 29% of all arthropod introductions (Rabitsch, 2010). Yet, not all alien insects are able to successfully colonize novel host plants, and understanding why some of them fail to do so can help guide nature conservation and the control of invasive species.

Generally, the successful colonization of a novel host by an herbivorous insect is affected by a number of factors, including phylogenetic relatedness of the novel plant to its original host plant (e.g., Odegaard et al., 2005; Ness et al., 2011; Karolewski et al., 2014), the duration of con-

tact between the novel partners (Brändle et al., 2008; Karolewski et al., 2017, but see Andow & Imura, 1994) and host specificity (Novotny et al., 2003; Roques et al., 2009; Walczak et al., 2017). The ability of an insect to successfully colonize new hosts is also strongly determined by the plant's physical, chemical, and phenological traits (Coley & Barone, 1996; Loranger et al., 2013; Bogdziewicz et al., 2018). Notably, leaves with a high specific leaf area (SLA), i.e., high leaf area to leaf mass ratio, which usually have a higher photosynthetic capacity, higher leaf nitrogen concentration and water content, and lower investment in structural defenses (Reich et al., 1997; Cornelissen et al., 2003) are more palatable to herbivores than leaves with a low SLA (Coley & Barone, 1996; Hanley et al., 2007). As a consequence of this well-established correlation between SLA and other traits of leaves, SLA is often used as a proxy for leaf palatability (Poorter et al., 2004; Whitfield et al., 2012).

In this study, we examined the host selection of an alien leaf miner *Phyllonorycter leucographella* (Zeller, 1850) on both its original host as well as on novel host plants in this

insect's alien range. The original host of this moth is the evergreen firethorn *Pyracantha coccinea* M. Roem (Triberti, 2007), cultivars of which are widely grown in urban green spaces. The moth and its original host are native to southern Europe and western Asia. The leaf miner was introduced inadvertently with plant material into several western European countries and then extended its range to the north (Šefrová, 2003). In Poland, the moth was discovered for the first time in 1999 (Baraniak & Walczak, 2000). Our previous study has shown that *P. leucographella* is able to colonize other taxa of the family Rosaceae (subfamily Maloideae; up to 75 novel hosts reported in Walczak et al., 2010). Yet, percentage infestation and the degree of developmental success of the leaf miner on novel host plants vary greatly, and it appears that this insect is unable to successfully establish on plants other than *P. coccinea* (Walczak et al., 2010). In this study, we aimed to investigate the factors responsible for this situation.

Based on our field observations, we predicted that the percentage infestation of the insect's original host is positively related to the leaf's SLA, because high-SLA leaves are usually nutritious and have thin cuticles (Burghardt & Riederer, 2006), both characteristics related to high offspring development success (Wright & Bourne, 1986). Next, if *P. leucographella* uses SLA as a cue to select best-quality leaves for oviposition on its original host plant, we predicted that this host selection process would also be followed when selecting novel host plants. However, because plants with high-SLA leaves in temperate Europe are often deciduous, such a host choice would be maladaptive because this leaf miner's larvae overwinter in leaves and deciduous plants shed their leaves before winter. If true, the transposition of the SLA cue from the original to novel hosts would be detrimental for the overwintering generation of this alien moth.

MATERIAL AND METHODS

Study sites and species

This study was done at two locations in western Poland: Adam Mickiewicz University Botanical Garden in Poznań (52°13'46"N, 21°0'44"E) and Kórnik Arboretum of the Institute of Dendrology of the Polish Academy of Sciences (52°14'30"N, 17°05'44"E). Both harbour diverse collections of trees and shrubs of the family Rosaceae. In a previous study, we observed that *P. leucographella* colonize only taxa belonging to the subfamily Maloideae (Walczak et al., 2010). Therefore, in this study, we included 175 species, varieties, hybrids and cultivars belonging to this subfamily (Table S1).

P. leucographella (Lepidoptera: Gracillariidae) is a monophagous species whose larvae mine the leaves of the evergreen firethorn, *Pyracantha coccinea* (Triberti, 2007). The native range of the leaf miner and its host plant includes southern Europe and western Asia (Šefrová, 2003; Seneta & Dolatowski, 2004). Females lay their eggs on the upper surface of a leaf. The larva initially feeds along the midrib, creating an epidermal corridor. The mine gradually widens into a silvery blotch and, finally, into a tentiform mine, causing the leaf to fold along the midrib. Unlike *Phyllonorycter corylifoliella* (Hübner, 1796), which is native to Poland, with which the alien moth shares some host plants, there are no black-brown specks in the mine. In western Poland, *P. leu-*

cographella has two generations per year. First-generation larvae are usually active in July, whereas the second, overwintering generation is observed from the end of August until April. The moth hibernates in the larval stage (Stigter & van Frankenhuyzen, 1991). Part of the population may overwinter in the pupal stage, but the first pupae appear in late October (Šefrová, 1999) when local deciduous plants shed their leaves.

Leaf sampling and measurement of specific leaf area

We estimated infestation by this moth in relation to the SLA value on five specimens of *P. coccinea*, growing in the Kórnik Arboretum. For this purpose, two randomly selected branches were cut off of each specimen in December 2016. To determine the variability in SLA, we divided each branch into three sections: basal, middle and apical, as the SLA values change with exposure to sun. For each section, the total number of leaves and the number of mined leaves were determined, which allowed us to calculate the percentage infestation. To measure the SLA of each branch section, we selected 10 leaves without signs of herbivore damage with sizes corresponding to those of the infested leaves. We selected leaves of similar size to infested ones, because infested leaves could not be used for SLA measurements. We treated them as surrogates of the infested leaves in the analysis. Then, 9–26 additional leaves were randomly selected to determine the average SLA value for each branch section. The number (9–26) of additional leaves sampled varied due to varying branch architecture.

To estimate the probability of infestation of novel hosts by the moth and the larvae's developmental success in relation to the SLA, we first estimated the SLA (leaf area per unit dry leaf mass: $\text{cm}^2 \text{g}^{-1}$) for 1–3 specimens of each plant taxon. These were single specimens for which we previously studied the host range of this moth and 1–2 additional specimens per plant taxon, depending on their availability in the collection (Walczak et al., 2010). Of the 175 taxa studied, 29 were evergreen or semi evergreen, and 146 were deciduous (Table S1). We collected whole twigs from each specimen and placed them in containers with water for transport to the laboratory. The same day, we took 3 fully expanded leaves to measure the SLA. For the analysis, we calculated the mean SLA for each taxon. This was done in August 2012 in the Botanical Garden in Poznań.

To assess novel host selection and moth development success, we randomly selected a single specimen from each of the plant taxa studied. At the beginning of July and at the end of August, for each specimen we randomly selected one twig, on which we counted 100 leaves from the top for further observation. We checked the leaves every 2 weeks, marking every mine and following its development. Next, we collected leaves with contracted mines to rear adults in the laboratory. We categorized development as successful if at least one adult moth was reared or if we found a pupal exuvium in the mine. We studied the developmental success of the first generation. We were not able to trace the entire development of the second generation, because in late October most host plants shed their leaves. Data for this generation were limited mainly to information on the presence or absence of mines. These surveys were conducted in the Botanical Garden in Poznań from July until October in 2002, 2004, and 2007.

We measured SLA by scanning leaves with an HP LaserJet 1320 scanner and measuring the leaf area in mm^2 using Win-Needle (version 3.5; Regent Instruments Inc., Quebec, Canada). All measurements were made on fresh material. We oven dried leaves at 65°C for 48 h, and weighed the dry mass on a BP210S Sartorius (Gottingen, Germany) analytical balance to the nearest

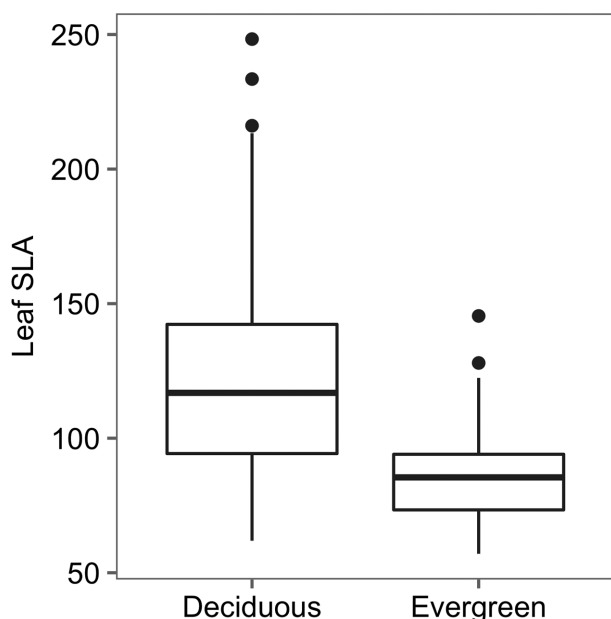


Fig. 1. Specific leaf area (SLA, $\text{cm}^2 \text{g}^{-1} \text{d.m.}$) of deciduous and evergreen species sampled in this study.

0.0001 g. We calculated SLA as the quotient of projected area of the fresh leaf and its dry mass ($\text{cm}^2 \text{g}^{-1}$).

Data analysis

We tested whether the percentage of leaves of *P. coccinea* infested by *P. leucographella* is related to SLA using a binomial, logit link, generalized linear mixed model (GLMM) with the branch nested within shrub ID included as a random effect. The response was the percentage of infested leaves sampled from a particular branch section, and the fixed effect was the mean log-transformed leaf SLA of that branch section.

Next, we evaluated whether host selection by *P. leucographella* of novel hosts is related to leaf traits. We built two binomial families, logit link, GLMMs with host selection as a response (0 = no signs of mine infestation by the focal insect on surveyed taxon, 1 = signs of mine infestation) and plant genus as a random effect. The inclusion of the genus as a random intercept allowed us to estimate SLA effects on focal responses within phylogenetic groups. In the first model, we included log-transformed SLA as a fixed effect. In the second model, we included foliar habit (evergreen vs. deciduous) as a fixed effect. We built separate models for these two explanatory variables because they were strongly correlated with one another (see Fig. 1). In both, year of sampling was included as an additional covariate, to account for potential non-independence of observations within the year or within location.

We tested whether leaf traits are related to larvae's developmental success using binomial, logit link GLMMs with genus included as a random effect. Here, the response was developmental success (0 = presence of mine without signs of adult emergence on surveyed taxon, 1 = an adult moth was reared or mine with signs of adult emergence). As previously, we built two separate models with log-transformed SLA (Model 1) or foliar habit (Model 2) and included fixed effects. Furthermore, year of sampling was included as an additional covariate, to account for potential non-independence of observations within the year or within location. We implemented all models using the lme4 package in R (Bates et al., 2015; R Development Core Team, 2017).

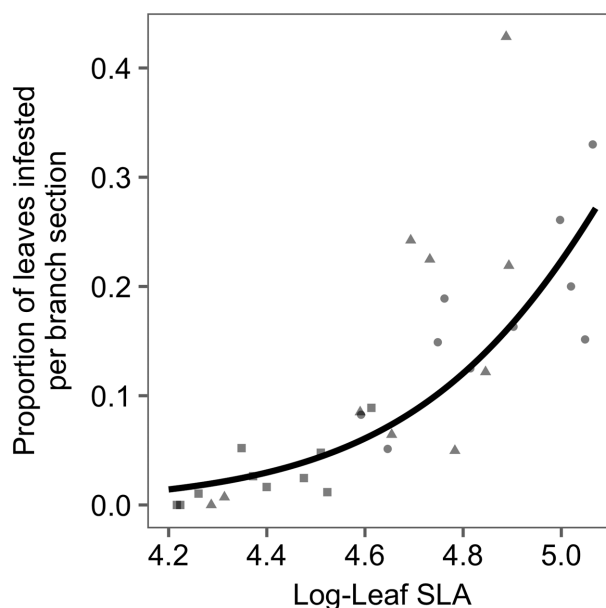


Fig. 2. Proportion of *P. coccinea* leaves infested by the leaf miner *P. leucographella* as a function of SLA. The curve denotes a significant mixed-effects logistic regression of the proportion infested vs. SLA. The dots represent the per-branch-section proportion of leaves infested vs. the average SLA of that branch section. Different symbols indicate different branch sections (circles – basal, triangles – middle, squares – apical).

RESULTS

The percentage of *P. coccinea* leaves infested by *P. leucographella* increased with the leaf's SLA ($t = 76.77$, $p < 0.001$). For low SLA values (~ 50), the percentage infestation was below 5%, and increased to over 30% for high SLA (200) leaves (Fig. 2).

The probability of *P. leucographella* infestation of a novel host plant increased significantly with the mean SLA of the host taxon ($z = 2.48$, $p = 0.01$). For low SLA values (~ 55), the probability of finding signs of mine infestation by *P. leucographella* equaled roughly 20%, and it increased to over 50% for taxa with SLA values over 200 (Fig. 3A). Furthermore, the probability of infestation by this insect was lower for evergreen ($\sim 10\%$) than for deciduous ($\sim 38\%$) species ($t = -2.61$, $p = 0.009$, Fig. 3B). Year effect was not significant ($p > 0.20$).

Similarly, the probability of successful development of *P. leucographella* on novel hosts increased with the mean SLA of the host taxon ($z = 2.60$, $p = 0.03$). For low SLA values, the probability of adult emergence was roughly 20%, but it increased to over 90% for leaves with high SLAs (Fig. 3C). In contrast, the probability of successful development from larva to adult was not related to the host plant's foliar habit ($z = -0.24$, $p = 0.80$). Year effect was not significant ($p > 0.20$).

DISCUSSION

The leaf miner *P. leucographella* selects leaves of *P. coccinea* according to their SLA values, and the percentage of leaves infested with this insect increases with leaf SLA. Generally, leaves with high SLAs have reduced structural

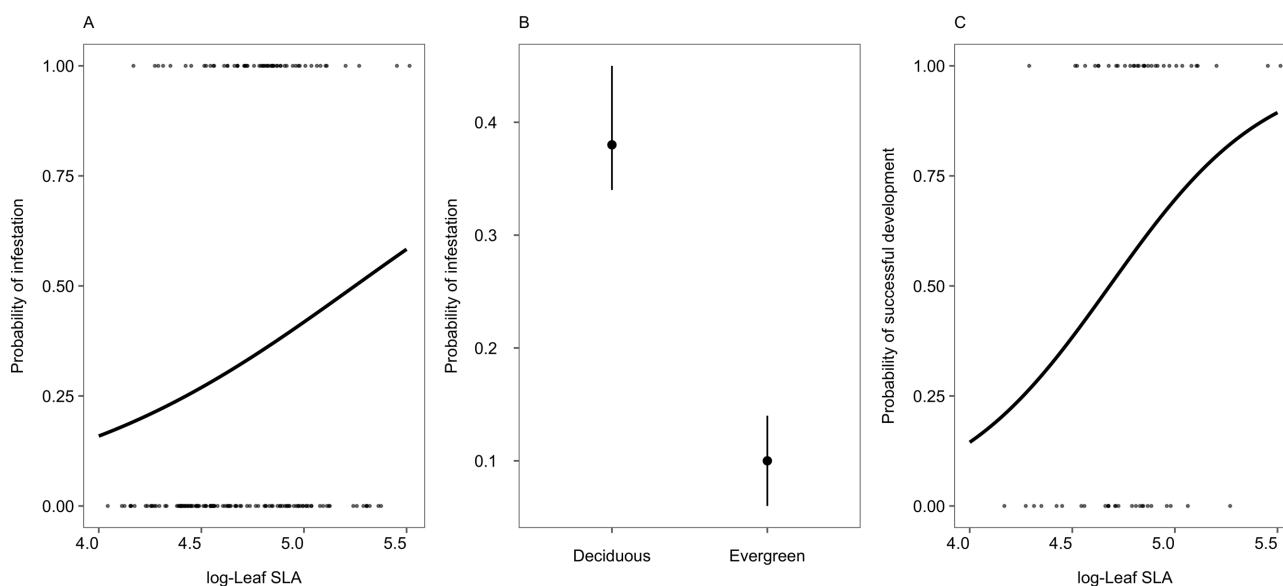


Fig. 3. Probability of infestation of plant taxa as a function of (A) mean leaf SLA, and (B) foliar habit. The whiskers attached to the data points in (B) indicate standard errors. (C) Probability of successful development of the moth as a function of mean leaf SLA of the taxa studied. The dots on (A) and (C) are data points – i.e., on (A), taxa infested with *P. leucographella* vs. those with no signs of infestation and on (C), infested taxa on which a larva developed into an adult vs. those with unsuccessful development. Estimates are derived from generalized linear mixed models (see Methods for details).

defenses and are more susceptible to damage caused by herbivores (Lei & Lechowicz, 1990; Schädler et al., 2003; Hanley et al., 2007; Karolewski et al., 2013). *P. leucographella* adults oviposit on the upper leaf surface and the larvae enter the epidermis through the cuticle and outer cell wall of the epidermis. The success of the penetration of the epidermis by newly hatched larvae is related to the thickness of the cell walls and cuticle (Wright & Bourne, 1986). Therefore, it appears that *P. leucographella* females prefer leaves with high SLA in order to increase the developmental success of their offspring.

The SLA value is also positively related to the probability of *P. leucographella* attacking a novel host plant. Thus, in the insect's new range, the host selection process appears to be based on the same cue that the insect utilizes to select leaves on its primary host plant. Furthermore, the probability for successful development of *P. leucographella* on novel hosts was positively related to the SLA value. Host plant quality is an important determinant of insect performance, like survivorship, developmental time and fecundity (Awmack & Leather, 2002; Muñoz et al., 2014; Wetzal et al., 2016). High nitrogen and water content of leaves, associated with high-SLA leaves, positively affect the performance of herbivores (Mattson & Scriber, 1987; Ojeda-Avila et al., 2003). In our system, the selection of high-SLA plants by the moth leads to high developmental success on novel host plants in the first (summer) generation. Yet, the utilization of this cue is likely to have a detrimental effect on the second (overwintering) generation.

Based on the pattern in our data and theory, we speculate that in selecting plants with high-SLA leaves for oviposition in the second generation is maladaptive in this insect's novel range. In temperate Europe, high SLA values are associated with deciduous plants that shed their leaves

in autumn (see Fig. 1). Therefore, although this was not tested in this study, the second-generation larvae that overwinter in the leaves presumably cannot survive winter. If true, these novel host plants need to be recolonized every year from the neighbouring primary host plants (*P. coccinea*). It is likely that this maladaptation is associated with the early stage of colonization, because insects do not have enough time to develop traits that would allow them to adapt to the new hosts (Schlaepfer et al., 2002; Harvey et al., 2010; Garcia-Robledo & Horvitz, 2012). However, natural selection may eventually tailor the alien species to fit the new environment. For example, the soapberry bug, *Jadera haematoloma*, evolved morphological and life history traits that increased its performance on new hosts (Carroll & Boyd, 1992; Carroll et al., 1997, 1998). Therefore, it appears possible that *P. leucographella* will adapt to its new environment, perhaps by adjusting the phenology of the second generation to allow complete development even on deciduous plants. As for now, there are no naturally occurring evergreen species outside of cultivation in Poland. Therefore, if this new adaptation happens, the so-called “noninvasive” species could suddenly spread widely to other hosts and natural plant communities and become even more troublesome.

This insect is considered to be host specific on *P. coccinea* (Triberti, 2007), however in the invaded area, under conditions of high population densities, it may also attack related plants in the family Rosaceae (Šefrová, 2005; Gröbler & Lewis, 2008; Walczak et al., 2010). This discrepancy may, on the one hand, result from the lack of research in its native range. On the other hand, it may reflect an ongoing adaptation process to a larger set of alternate host plants available in urban greenery (towards oligophagy).

The alien leaf miner *P. leucographella* currently spreads following its primary host plant *P. coccinea* (Nash et al., 1995). Yet, the range of this plant is currently limited to urban and suburban areas where it tends to be planted. Based on our study we hypothesize that the maladaptive selection of novel host plants by this insect reduces its invasiveness by preventing its establishment on native plants. As a consequence, it is likely that this maladaptive selection process prevents permanent settling on new hosts in urban environments and hinders this species colonization of natural plant communities. Further studies should investigate the potential for natural selection to overcome the maladaptive host selection process in order to increase our understanding of possible changes in insect spread dynamics.

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Table S1. Woody rosaceous plants included in this study. Abbreviations: D – deciduous, E – evergreen, SE – semi-evergreen.

	Plant name	Status in Poland	Foliar habit	Mine infestation
1	<i>Amelanchier alnifolia</i> (Nutt.) Nutt.	Alien	D	No
2	<i>Amelanchier laevis</i> Wiegand	Alien	D	No
3	<i>Amelanchier spicata</i> (Lam.) K. Koch	Alien	D	No
4	× <i>Amelastorbus jackii</i> Rehder	Hybrid	D	No
5	<i>Aronia ×prunifolia</i> (Marshall) Rehder	Hybrid	D	No
6	<i>Chaenomeles cathayensis</i> (Hemsl.) C.K. Schneid.	Alien	D	No
7	<i>Chaenomeles japonica</i> (Thunb.) Lindl. ex Spach	Alien	D	Yes
8	<i>Chaenomeles speciosa</i> (Sweet) Nakai	Alien	D	No
9	<i>Chaenomeles ×superba</i> (Frahm) Rehder	Hybrid	D	No
10	<i>Cotoneaster acutifolius</i> Turcz.	Alien	D	No
11	<i>Cotoneaster adpressus</i> Bois	Alien	D	Yes
12	<i>Cotoneaster adpressus</i> 'Little Gem'	Cultivar	D	No
13	<i>Cotoneaster affinis</i> Lindl.	Alien	D	No
14	<i>Cotoneaster aitchinsonii</i> C.K. Schneid.	Alien	D	Yes
15	<i>Cotoneaster albokermesinus</i> J. Fryer et B. Hylmö	Alien	D	No
16	<i>Cotoneaster ambiguus</i> Rehder et E.H. Wilson	Alien	D	Yes
17	<i>Cotoneaster amoenus</i> E.H. Wilson	Alien	E	No
18	<i>Cotoneaster apiculatus</i> Rehder et E.H. Wilson	Alien	D	No
19	<i>Cotoneaster armenus</i> Pojark.	Alien	D	No
20	<i>Cotoneaster ascendens</i> Flinck et B. Hylmö	Alien	D	No
21	<i>Cotoneaster astrophoros</i> J. Fryer et E.C. Nelson	Alien	E	No
22	<i>Cotoneaster atropurpureus</i> Flinck et B. Hylmö	Alien	D	No
23	<i>Cotoneaster atropurpureus</i> 'Variegatus'	Cultivar	D	No
24	<i>Cotoneaster bacillaris</i> Wall. ex Lindl.	Alien	D	No
25	<i>Cotoneaster boisianus</i> G. Klotz	Alien	D	No
26	<i>Cotoneaster borealichinensis</i> (Hurus.) Hurus.	Alien	D	No
27	<i>Cotoneaster bradyi</i> E.C. Nelson et J. Fryer	Alien	D	No
28	<i>Cotoneaster bullatus</i> Bois	Alien	D	No
29	<i>Cotoneaster calocarpus</i> (Rehder et E.H. Wilson) Flinck et B. Hylmö	Alien	D	No
30	<i>Cotoneaster cashmiriensis</i> G. Klotz	Alien	E	No
31	<i>Cotoneaster cinerascens</i> (Rehder) Flinck et B. Hylmö	Alien	E or SE	No
32	<i>Cotoneaster cochleatus</i> (Franch.) G. Klotz	Alien	E	No
33	<i>Cotoneaster congestus</i> 'Nanus'	Cultivar	E	No
34	<i>Cotoneaster conspicuus</i> Comber ex Marquand	Alien	E	Yes

Table S1 (continued).

	Plant name	Status in Poland	Foliar habit	Mine infestation
35	<i>Cotoneaster dammeri</i> C.K. Schneid	Alien	E	No
36	<i>Cotoneaster dammeri</i> 'Major'	Cultivar	E	No
37	<i>Cotoneaster dielsianus</i> E. Pritz.	Alien	D	Yes
38	<i>Cotoneaster discolor</i> Pojark.	Alien	D	No
39	<i>Cotoneaster divaricatus</i> Rehder et E.H. Wilson	Alien	D	Yes
40	<i>Cotoneaster elatus</i> 'Ruby'	Cultivar	E or SE	No
41	<i>Cotoneaster fangianus</i> T.T. Yü	Alien	D	No
42	<i>Cotoneaster floccosus</i> (Rehder et E.H. Wilson) Flinck et B. Hylmö	Alien	E	No
43	<i>Cotoneaster foveolatus</i> Rehder et E.H. Wilson	Alien	D	No
44	<i>Cotoneaster franchetii</i> Bois	Alien	E or SE	No
45	<i>Cotoneaster giraldii</i> Flinck et B. Hylmö	Alien	D	No
46	<i>Cotoneaster glacialis</i> Panigrahi et Kumar	Alien	E	No
47	<i>Cotoneaster harrismithii</i> Flinck et B. Hylmö	Alien	D	No
48	<i>Cotoneaster hissaricus</i> Pojark.	Alien	D	No
49	<i>Cotoneaster hjelmqvistii</i> Flinck et B. Hylmö	Alien	D	No
50	<i>Cotoneaster horizontalis</i> Decne.	Alien	D	Yes
51	<i>Cotoneaster hsingshangensis</i> J. Fryer et B. Hylmö	Alien	D	Yes
52	<i>Cotoneaster hummelii</i> J. Fryer et B. Hylmö	Alien	D	No
53	<i>Cotoneaster hupehensis</i> Rehder et E.H. Wilson	Alien	D	No
54	<i>Cotoneaster hurusawaiianus</i> G. Klotz	Alien	D	Yes
55	<i>Cotoneaster hylmoei</i> Flinck et J. Fryer	Alien	E or SE	No
56	<i>Cotoneaster induratus</i> J. Fryer et B. Hylmö	Alien	SE	No
57	<i>Cotoneaster insignis</i> Pojark.	Alien	D	Yes
58	<i>Cotoneaster integerrimus</i> Medik.	Native	D	No
59	<i>Cotoneaster integrifolius</i> Buch.-Ham. ex Hook.f.	Alien	E	No
60	<i>Cotoneaster kitaibelii</i> Hort.	Alien	D	No
61	<i>Cotoneaster laxiflorus</i> Jacq. ex Lindl.	Alien	D	No
62	<i>Cotoneaster lucidus</i> Schldl.	Alien	D	Yes
63	<i>Cotoneaster ludlowii</i> G. Klotz	Alien	D	No
64	<i>Cotoneaster magnificus</i> J. Fryer et B. Hylmö	Alien	D	No
65	<i>Cotoneaster megalocarpus</i> auct.	Alien	D	No
66	<i>Cotoneaster melanocarpus</i> G. Lodd. ex C. K. Schneid.	Native	D	Yes
67	<i>Cotoneaster microphyllus</i> Wall. ex Lindl.	Alien	E	No
68	<i>Cotoneaster miniatus</i> Flinck et B. Hylmö	Alien	D	No
69	<i>Cotoneaster monopyrenus</i> (W.W. Sm.) Flinck et B. Hylmö	Alien	D	Yes
70	<i>Cotoneaster moupinensis</i> Franch.	Alien	D	No
71	<i>Cotoneaster multiflorus</i> Bunge	Alien	D	No
72	<i>Cotoneaster nanshan</i> Mottet	Alien	D	Yes
73	<i>Cotoneaster nepalensis</i> André	Alien	D	Yes
74	<i>Cotoneaster nitens</i> Rehder et E.H. Wilson	Alien	D	Yes
75	<i>Cotoneaster nummularioides</i> Pojark.	Alien	D	No
76	<i>Cotoneaster obscurus</i> Rehder et E.H. Wilson	Alien	D	Yes
77	<i>Cotoneaster oliganthus</i> Pojark.	Alien	D	No
78	<i>Cotoneaster otto-schwarzii</i> G. Klotz	Alien	D	No
79	<i>Cotoneaster polyanthemus</i> E.L. Wolf	Alien	D	No
80	<i>Cotoneaster procumbens</i> G. Klotz	Alien	E	Yes
81	<i>Cotoneaster przewalski</i> Pojark.	Alien	D	Yes
82	<i>Cotoneaster purpurascens</i> J. Fryer et B. Hylmö	Alien	D	No
83	<i>Cotoneaster racemiflorus</i> Booth ex Bosse	Alien	D	No
84	<i>Cotoneaster radicans</i> G. Klotz	Alien	E	No
85	<i>Cotoneaster rehderi</i> Pojark.	Alien	D	Yes
86	<i>Cotoneaster roseus</i> Edgew.	Alien	D	No
87	<i>Cotoneaster rugosus</i> E. Pritz. ex Diels.	Alien	D	Yes
88	<i>Cotoneaster salicifolius</i> Franch.	Alien	E or SE	No
89	<i>Cotoneaster salicifolius</i> 'Repens'	Alien	E or SE	No
90	<i>Cotoneaster salwinensis</i> G. Klotz	Alien	D	No
91	<i>Cotoneaster scandinavicus</i> B. Hylmö	Alien	D	No
92	<i>Cotoneaster shansiensis</i> Flinck et B. Hylmö	Alien	D	Yes
93	<i>Cotoneaster sherriffii</i> G. Klotz	Alien	E	No
94	<i>Cotoneaster sikangensis</i> Flinck et B. Hylmö	Alien	D	No
95	<i>Cotoneaster simonsii</i> Hort. ex Baker	Alien	D	Yes
96	<i>Cotoneaster splendens</i> Flinck et B. Hylmö	Alien	D	Yes
97	<i>Cotoneaster sternianus</i> (Turill) Boom	Alien	E	No
98	<i>Cotoneaster subacutus</i> Pojark.	Alien	D	Yes
99	<i>Cotoneaster x suecicus</i> G. Klotz	Hybrid	E	Yes
100	<i>Cotoneaster x suecicus</i> 'Ursynów'	Cultivar	E	No
101	<i>Cotoneaster x suecicus</i> 'Coral Beauty'	Cultivar	E	No
102	<i>Cotoneaster tauricus</i> Pojark.	Alien	D	No
103	<i>Cotoneaster tomentellus</i> Pojark.	Alien	D	No
104	<i>Cotoneaster tomentosus</i> (Aiton) Lindl.	Native	D	No
105	<i>Cotoneaster tumeticus</i> Pojark.	Alien	D	No
106	<i>Cotoneaster veitchii</i> G. Klotz	Alien	D	No
107	<i>Cotoneaster verokotschyi</i> J. Fryer et B. Hylmö	Alien	D	No
108	<i>Cotoneaster villosulus</i> Flinck et B. Hylmö	Alien	D	Yes
109	<i>Cotoneaster wardii</i> W.W. Sm.	Alien	E	No
110	<i>Cotoneaster zabelii</i> C.K. Schneid.	Alien	D	Yes
111	<i>Crataegus x media</i>	Hybrid	D	No
112	<i>Crataegus x media</i> 'Candidoplena'	Cultivar	D	No
113	<i>Crataegus x media</i> 'Paul's Scarlet'	Cultivar	D	No

Table S1 (continued).

	Plant name	Status in Poland	Foliar habit	Mine infestation
114	<i>Crataegus nigra</i> Pall. ex Steud.	Alien	D	No
115	<i>Crataegus altaica</i> (Loudon) Lange	Alien	D	Yes
116	<i>Crataegus chlorosarca</i> Maxim.	Alien	D	No
117	<i>Crataegus crus-galli</i> L.	Alien	D	Yes
118	<i>Crataegus flabellata</i> K. Koch	Alien	D	Yes
119	<i>Crataegus intricata</i> Lange	Alien	D	Yes
120	<i>Crataegus monogyna</i> Jacq.	Native	D	Yes
121	<i>Crataegus persimilis</i> 'Splendens'	Cultivar	D	Yes
122	<i>Crataegus pinnatifida</i> Bunge	Alien	D	No
123	<i>Crataegus pinnatifida</i> Bunge var. <i>major</i> N.E. Br.	Variety	D	Yes
124	<i>Crataegus punctata</i> Jacq.	Alien	D	Yes
125	<i>Crataegus rhipidophylla</i> Gand.	Native	D	Yes
126	<i>Crataegus succulenta</i> (Link) Schrad.	Alien	D	Yes
127	× <i>Crataemespilus grandiflora</i> (J. Sm.) E.G. Camus	Hybrid	D	Yes
128	+ <i>Crataegomespilus dardarii</i> 'Asnieressi'	Cultivar	D	Yes
129	<i>Cydonia oblonga</i> Mill.	Alien	D	Yes
130	<i>Exochorda korolkowii</i> Lavallee	Alien	D	No
131	<i>Holodiscus discolor</i> (Pursh) Maxim.	Alien	D	No
132	<i>Malus</i> 'Jadwiga'	Cultivar	D	No
133	<i>Malus</i> 'Flame'	Cultivar	D	No
134	<i>Malus</i> 'Hillieri'	Cultivar	D	No
135	<i>Malus</i> 'Lemoinei'	Cultivar	D	No
136	<i>Malus</i> 'Professor Sprenger'	Cultivar	D	No
137	<i>Malus baccata</i> (L.) Borkh.	Alien	D	No
138	<i>Malus floribunda</i> Siebold ex Van Houtte	Alien	D	Yes
139	<i>Malus fusca</i> (Raf.) C.K. Schneid.	Alien	D	Yes
140	<i>Malus</i> × <i>hartwigii</i> Koehne	Hybrid	D	No
141	<i>Malus hupehensis</i> (Pamp.) Rehder	Alien	D	Yes
142	<i>Malus pumila</i> Mill.	Alien	D	Yes
143	<i>Malus</i> × <i>purpurea</i> (Barbier et al.) Rehder	Hybrid	D	No
144	<i>Malus</i> × <i>purpurea</i> 'Szafer'	Cultivar	D	Yes
145	<i>Malus sargentii</i> Rehder	Alien	D	Yes
146	<i>Malus sieboldii</i> (Rehder) Fiela var. <i>arborescens</i> Rehder	Variety	D	No
147	<i>Malus</i> × <i>soulardii</i> (Bailey) Britton	Hybrid	D	Yes
148	<i>Malus transitoria</i> (Batalin) C.K. Schneid.	Alien	D	Yes
149	<i>Malus tschonoskii</i> (Rehder) C.K. Schneid.	Alien	D	Yes
150	<i>Malus</i> 'Hyslop'	Cultivar	D	No
151	<i>Mespilus germanica</i> L.	Alien	D	No
152	<i>Photinia villosa</i> (Thunb.) DC.	Alien	D	Yes
153	<i>Pseudocydonia sinensis</i> (Thouin) C.K. Schneid.	Alien	SE	No
154	<i>Pyracantha coccinea</i> M. Roem.	Alien	E	Yes
155	<i>Pyrus</i> × <i>canescens</i> Spach	Hybrid	D	No
156	<i>Pyrus caucasica</i> Fedorov	Alien	D	No
157	<i>Pyrus communis</i> L.	Alien	D	No
158	<i>Pyrus salicifolia</i> Pall.	Alien	D	No
159	<i>Pyrus salicifolia</i> 'Pendula'	Cultivar	D	No
160	<i>Sorbocotoneaster pozdnyakovii</i> Pojark.	Alien	D	No
161	<i>Sorbus americana</i> Marshall	Alien	D	No
162	<i>Sorbus aria</i> (L.) Crantz	Native	D	No
163	<i>Sorbus aria</i> 'Lutescens'	Cultivar	D	No
164	<i>Sorbus aucuparia</i> L.	Native	D	Yes
165	<i>Sorbus aucuparia</i> 'Xanthocarpa'	Cultivar	D	No
166	<i>Sorbus cashmiriana</i> Hedl.	Alien	D	Yes
167	<i>Sorbus commixta</i> Hedl.	Alien	D	No
168	<i>Sorbus domestica</i> L.	Alien	D	No
169	<i>Sorbus intermedia</i> (Ehrh.) Pers.	Native	D	Yes
170	<i>Sorbus mougeotii</i> Soy.-Will. et Godr.	Alien	D	Yes
171	<i>Sorbus serotina</i> Koehne	Alien	D	No
172	<i>Sorbus torminalis</i> (L.) Crantz	Native	D	Yes
173	<i>Sorbus umbellata</i> (Desf.) Fritsch var. <i>cretica</i> (Lindl.) C.K. Schneid.	Variety	D	Yes
174	<i>Sorbus vilmorinii</i> C.K. Schneid.	Alien	D	No
175	<i>Stranvaesia davidiana</i> Decne.	Alien	D	No