

INVADING THE MEDITERRANEAN: STUDY OF *SOLANUM ELAEAGNIFOLIUM*, A SUCCESSFUL INVASIVE PLANT FROM C. AMERICA

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Abstract

The number of alien (non-native) organisms in natural habitats is growing. They are introductions from other habitats, which often share similar climatic conditions. Aliens that adversely affect the habitat they invade ecologically, environmentally or economically are called invasives. Typical pathways of invasion are the pet trade, horticultural trade, shipping industry (ballast water), agricultural produce and biological control. We focus our research on the distribution and impact of the Central American invasive plant *Solanum elaeagnifolium* on the native flora and fauna of Greece. In particular we map the plant's current distribution in the country and examine its' impact on the pollination of the native species *Glaucium flavum* and the infestation of the potato crop with the Colorado potato beetle (CPB) on Lesvos Island.

We analysed questionnaires sent to state-employed and private agronomists in all 52 prefectures of Greece. According to our survey, *S. elaeagnifolium* is present in 24 of the 33 prefectures from where we received filled out questionnaires. We complemented our results with historical data, which confirm the plant's presence in 15 prefectures also highlighted by our survey and add an additional seven invaded prefectures. Our research shows that flowers of our native indicator plant, *G. flavum*, receive significantly fewer visits in populations that are invaded by *S. elaeagnifolium*, which may impact seed set. This has important conservation implications as pebble and shingle beaches and their perennial vegetation, to which *G. flavum* belongs have been designated as special areas of conservation in Annex I of the EU Habitat Directive 92/43/EEC. Furthermore, we show first evidence that *S. elaeagnifolium* may act as a stepping stone for CPB facilitating the infestation of the summer potato crop, which would have grave economical impacts.

Key words: invasive, competition, pollination, Colorado potato beetle, *Glaucium flavum*

1 Introduction

1.1 Biological invasion

Biological invasion is a main driver for global biodiversity loss and is increasing through globalization, trade and tourism. Typical pathways of invasion are the pet trade, horticultural trade, shipping industry (ballast water), agricultural produce and biological control. Aliens that spread and adversely affect the habitat they invade ecologically, environmentally or economically are called invasives. Biological invasions cost the U.S. economy alone over \$100 billion per year in losses, damages, and control (Pimentel et al. 2000). Biological and ecological traits of an introduced species are important factors and decide whether the alien species establishes and spreads in the new habitat or not. In plants, traits that can facilitate establishment are e.g. fast growth, deep root system, vegetative as well as sexual reproduction, tolerance of a wide range of environmental conditions, prolonged flowering, early sexual maturity, high reproductive output and dispersal. Kolar and Lodge (2001) showed that from a list of invasive and non-invasive species 86% of the invasive species could be identified on the basis of their traits alone. Most alien plants have left behind their enemies (herbivores and pathogens), which often explains their increased competitive ability (Maron and Vila 2001). In this study we generate a new distribution map of the invasive *Solanum elaeagnifolium* (Cav.) based on questionnaires sent to agronomists in all prefectures of Greece and historical data.

1.2 Impact on native plants

Invasive plants threaten biodiversity and ecosystem functioning (Pimentel et al. 2001, Traveset and Richardson 2006, Bjercknes et al. 2007), because they may displace native plants and crop species due to competition for space, nutrients, water and light (Wardle et al. 1994, Weihe and Neely 1997, Mack and D'Antonio 1998). They can also compete with the native flora for pollination services (Brown and Mitchell 2001, Chittka and Schürkens 2001, Brown et al. 2002, Aigner 2004, Moragues and Traveset 2005, Totland et al. 2006, see Bjercknes et al. 2007 for a short review). This may lead to lower seed set in the natives (Chittka

and Schürkens 2001, Brown et al. 2002, Moragues and Traveset 2005, Totland et al. 2006). Invasives could attract pollinators that were previously monopolized by the native species, which could lead to lower visitation rates to the natives, the deposition of heterospecific (foreign) pollen (Lopezaraiza-Mikel et al. 2007) and subsequently to reduction in seed set (Jacobi et al. 2005, Larson et al. 2006). However, there are also cases where invasives facilitate the pollination of natives (Grabas and Laverly 1999, Larson et al. 2006) or have no effect (Aigner 2004, Totland et al. 2006). Invasives' flowers constitute in themselves a resource for the pollinators, which could lead to an overall increase in pollinator abundance, diversity, geographic range or even duration of their foraging season and so potentially facilitate the pollination of the native plants (Memmott and Waser 2002, Feldman et al. 2004).

Here we examine the impact of the silverleaf nightshade, *S. elaeagnifolium* (Cavanilles), an invasive to the Mediterranean from Central America, on the visitation of the native yellow-horned poppy, *Glaucium flavum* (Crantz). *G. flavum* co-flowers and shares pollinators with the invasive during summer (May-August) and is found along sections of the Mediterranean coast, where it is part of the perennial vegetation of stony beaches.

1.3 The Colorado potato beetle, *Solanum elaeagnifolium* and the cultivation of potato

The Colorado potato beetle (CPB), *Leptinotarsa decemlineata* (Say), is the most devastating defoliator of potatoes worldwide. With an economic threshold of only one adult beetle per plant (Weber 2003), chemical control is crucial in many countries to avoid a major loss of yield. Originally native to Mexico, CPB now occurs in much of the US, Asia and Europe and arrived in Greece in 1963. CPB is oligophagous and it is well documented that its' populations vary geographically in host plant affinity (Hsiao 1978, De Wilde and Hsiao 1981, Hsiao 1981, 1982, Hsiao 1985, Hare and Kennedy 1986, Horton and Capinera 1988b, Forister et al. 2007). While CPB found in northern, central, and eastern US, Europe and Asia predominantly feed on cultivated potatoes, many populations in the Southwestern US and in Mexico infest native hosts such as *Solanum rostratum* (Dunal), *Solanum angustifolium* (Miller) and *S. elaeagnifolium* (Arizona only) (Hsiao 1978).

S. elaeagnifolium was first recorded on the island of Lesbos, Greece in 1975 (Economidou and Yannitsaros 1975) while according to potato growers the arrival of CPB on Lesbos can be dated back to approximately 1995. Both, plant and insect had therefore co-existed for more than a decade when this study was carried out. The extended growing season on Lesbos and many other parts of Greece allows the cultivation of two potato crops per year. The first crop is planted in March and harvested in late June to early July; the latter is planted in early August and harvested in late November to early December. While the spring crop usually harbours large numbers of CPB throughout cultivation, and triggers frequent insecticide applications, the summer crop is generally free of infestation. This can be attributed to the lack of alternate food plants between the two crops, because the absence of a suitable host plant can trigger diapause in adult CPB (Horton and Capinera 1988a). It has been suggested that *S. elaeagnifolium* could support plant pests such as CPB in some areas (Hsiao 1982, Boyd et al. 1984, Roche 1991), but so far the implications for potato cultivation near populations of *S. elaeagnifolium* have not been investigated. We know from laboratory no-choice tests that CPB can fulfill a full life cycle on whole *S. elaeagnifolium* plants (unpublished data). In the present study we aim to (i) identify if and when CPB feeds on wild *S. elaeagnifolium* on Lesbos, Greece; and (ii) assess whether *S. elaeagnifolium* can facilitate CPB infestation of the summer potato crop by acting as a stepping stone host.

2 Methodology

2.1 The study plants

S. elaeagnifolium is native to South and Central America and probably originated in Mexico and the Southwestern US (Boyd et al. 1984). It is a known invasive in all countries of the Mediterranean Basin, Australia, Chile, Australia, India, New Zealand, Pakistan, Puerto Rico, South Africa, Taiwan and Zimbabwe (Boyd et al. 1984, Bouhache and Tanji 1985, Mekki 2007). It is also a listed noxious weed in 21 states of the US, some of which are within the plants native range (Roche 1991, Mekki 2007). *S. elaeagnifolium* is deep-rooted, which is the main reason why control with herbicides has shown only limited success

(Eleftherohorinos et al. 1993, Baye et al. 2007). Silverleaf nightshade lowers crop yield through competition (Boyd and Murray 1982), may lower the quality of hay taken from infested fields (Boyd et al. 1984), and is toxic to livestock. *S. elaeagnifolium* can spread by seed and root fragments (Boyd and Murray 1982). The flowers have poricidal anthers and are pollinated by insects (Buchmann and Cane 1989). Individual berries produce 24 to 149 seeds (Boyd and Murray 1982), which can add up to 5 million to 100 million seeds per acre (Cooley and Smith 1971). Seeds may be dispersed by animal faeces, water, machinery and agricultural produce and dried plants may also blow like tumbleweeds, spreading seed along the way (Boyd et al. 1984). *G. flavum* is a perennial herb that occurs along the Mediterranean shores and the coasts of W. Europe in shingle or stable pebbles just above the beach (Thanos et al. 1989). Pebble and shingle beaches and their perennial vegetation have been designated as special areas of conservation in Annex I of the EU Habitat Directive 92/43/EEC (EU 1992).

2.2 Distribution of *Solanum elaeagnifolium* in Greece

In 2007, we sent questionnaires by fax and letter to state-employed and private agronomists in all 52 prefectures of Greece containing a picture of a flowering *S. elaeagnifolium* plant and stating the scientific as well as all common names of the plant asking whether it was present or absent in their prefecture. The questionnaires were analysed and a distribution map was generated on the basis of the replies. The map was complemented by historical distribution data from Boratynski et al. (1992), which was converted from single record data to binary presence/absence data in prefectures in order to be comparable with our survey data.

2.3 Impact of *Solanum elaeagnifolium* on the native *Glaucium flavum*

Observations of the pollinator visits to the flowers of *G. flavum* were carried out on two paired sites: beaches near Plomari and Skala Eresou with each one containing one invaded (38°58'15.77"N, 26°22'55.93"E and 39°8'20.27"N, 25°55'18.53"E, respectively) and one uninvaded (38°59'8.86"N, 26°18'53.12"E and 39°6'26.82"N, 25°57'53.17"E, respectively) site. The invaded and uninvaded sites within a pair were at least 5km apart and the two pairs were 40km apart.

Visits to the flowers of *S. elaeagnifolium* were observed in the two invaded sites. Observation plots (1m x 1m) were established randomly on observation days along a 50m transect in each invaded and uninvaded site so that every plot contained at least one flowering plant of *G. flavum* or *S. elaeagnifolium*. In each of four sampling rounds a minimum of six plots were observed per species in each of four sites in the case of *G. flavum* and two sites in case of *S. elaeagnifolium*. Observations were carried out in mid June, mid July, early August and late August 2006. In total we performed observations in 51 plots in uninvaded sites containing 83 *G. flavum* plants and 275 flowers, and in 62 plots in invaded sites containing 83 *G. flavum* plants and 443 flowers. In addition, we carried out observations in 63 plots in invaded sites containing 1365 *S. elaeagnifolium* flowers. Insect visitation to flowers was recorded for 3 min periods per plot and observations took place between 8.30 and 13.00 on sunny and calm days. In each census, in each observation plot, we recorded the total number of flowers present, the number of flowers visited and the insect visitors. The flower visitors were identified at least to family level in bees when species or genus was not known.

To analyse the visitation data we carried out an order-dependent (type I) log-linear analysis of covariance using a negative binomial error structure with log link in Proc Genmod within SAS 9.1, with site status as fixed factor (2 levels: invaded/ uninvaded) and flower abundance as covariate to account for the correlation between flower abundance and site status. Flower abundance was fitted first and the site status factor was fitted to the remaining unexplained variance. Overdispersion was accounted for. The analysis was based on the number of flower visits per plant.

2.4 *Solanum elaeagnifolium* and potato cultivation

The phenology of CPB on *S. elaeagnifolium* was assessed weekly from May to November in Arisvi where potatoes are cultivated near a population of *S. elaeagnifolium*. For the weekly CPB density surveys a minimum of 36 *S. elaeagnifolium* plants were chosen randomly for each survey. In order to investigate whether CPB can infest summer potato crops and if this is correlated with the distance to the nearest

population of *S. elaeagnifolium*, we surveyed 10 summer potato fields on a weekly basis around Arisvi from early October to November 2007. The distances of the surveyed fields to the nearest population of *S. elaeagnifolium* were 380m, 500m, 660m, 2000m, 4500m, 4600m, 4700m, 4750m, 5400m and 5600m. The choice of field sites was limited by the number of available potato fields and the presence of *S. elaeagnifolium*. We recorded all egg clusters, first to third instar larvae, fourth instar larvae and adult beetles on 20 potato plants on each visit.

3 Results

3.1 Distribution of *Solanum elaeagnifolium* in Greece

We received back filled out questionnaires from 33 prefectures. According to this survey, *S. elaeagnifolium* is present in 24 of those 33 prefectures. We compared these records with historical data from Boratynski et al. (1992), who report the plant's presence in 15 prefectures also highlighted by our survey and an additional seven prefectures from where we had no data. A distribution map for Greece was then generated using the data from both sources (Figure 1).

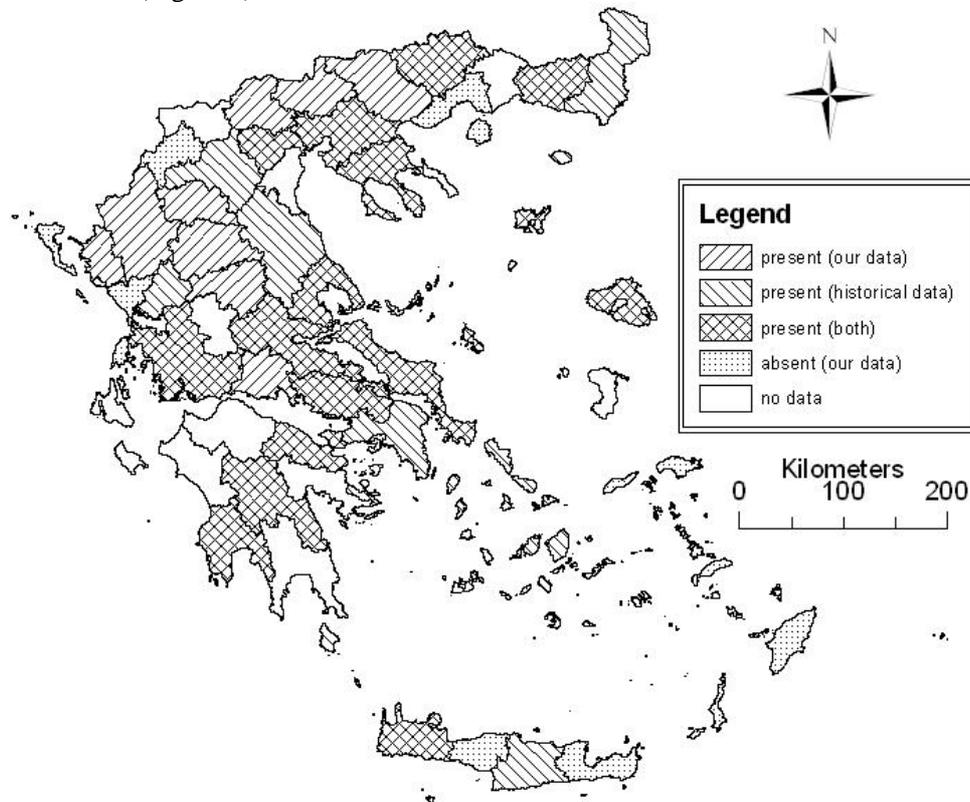


Figure 1: Distribution map of *S. elaeagnifolium* based on our questionnaire survey and historical data.

3.2 Impact of *Solanum elaeagnifolium* on native *Glaucium flavum*

A total of 47 *G. flavum* flowers were observed to have visits in the invaded sites and 122 *G. flavum* flowers were observed to have visits in the uninvaded sites (Table 1). *G. flavum* visitation was positively affected by *G. flavum* flower abundance ($F_{1,112} = 13.84$, $P < 0.001$). After accounting for the effect of flower abundance, the effect of site status (invaded/ uninvaded) on flower visitation is still significant ($F_{1,112} = 4.04$, $P = 0.048$). Each flower received on average 3.42 visits/ hour in the invaded and 5.51 visits/ hour in the uninvaded sites during the hours of observation.

Table 1: Main results from flower observations in invaded and uninvaded sites.

	UNINVADED	INVADED	
	<i>G. flavum</i>	<i>G. flavum</i>	<i>S. elaeagnifolium</i>
Plots	62	51	63
No of flowers	443	275	1635
Visited flowers	122	47	156
Flower visitation rate ^{-h}	5.51	3.42	1.91

All recorded visits in the invaded sites were by bees and 97.54 % of visits in the uninvaded sites were by bees (2.46 % fly visits). In the uninvaded sites, the number of visits to *G. flavum* flowers by *Amegilla* spp. accounted for almost 50% of all visits compared to just 10% in invaded sites (Figure 2). In contrast to the uninvaded sites, *G. flavum* was mainly visited by *Xylocopa iris* and *X. violacea*, as well as Megachilid bees in the invaded sites, which accounted for over 50% of the total visits.

A total of 156 *S. elaeagnifolium* flowers were visited in the invaded sites. *Amegilla* spp. accounted for almost 75% of all visits to *S. elaeagnifolium* flowers.

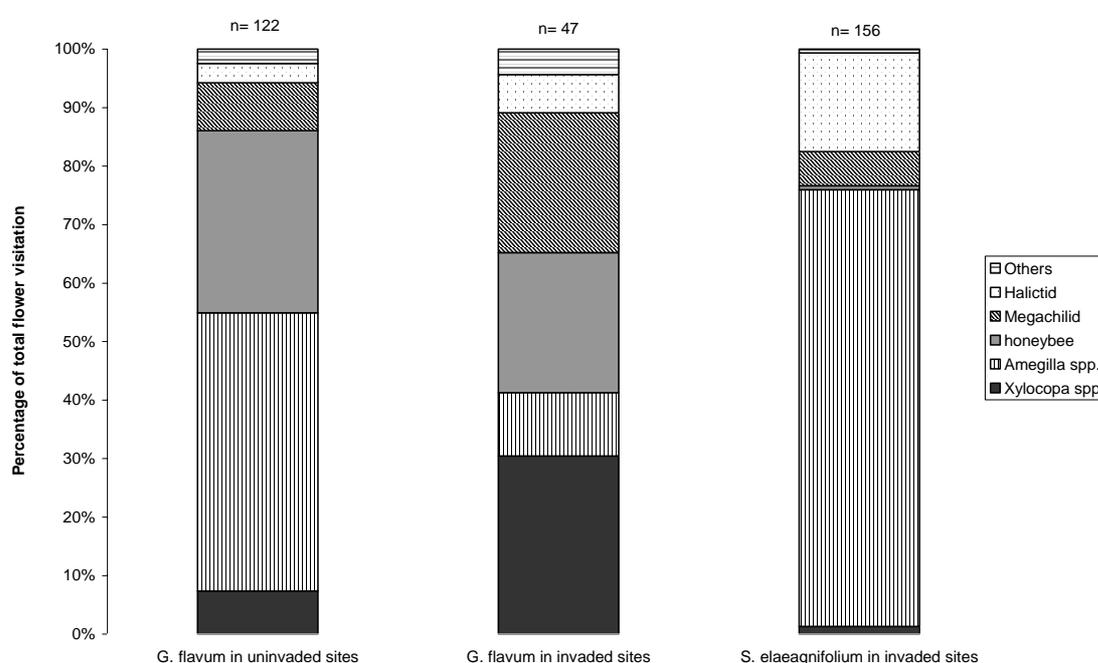


Figure 2: Composition of flower visitors in uninvaded and invaded sites.

3.3 *Solanum elaeagnifolium* and potato cultivation

Potatoes were harvested from late June to early July 2007 in Arisvi, and the first CPB appeared on the population of *S. elaeagnifolium* in late June as soon as the adjacent potato field had been harvested (Figure 3). During the following two weeks of harvest the number of CPB on *S. elaeagnifolium* continued to rise. In mid July, when all of the fields within 500m had been harvested, the density started to fall until late July when no more beetles were found on *S. elaeagnifolium*. In the following weekly censuses no further beetles were recorded until November, at which time very low beetle densities were found on *S. elaeagnifolium*.

CPB were only found in one field on the summer potato crop at a distance of 660m to the nearest population of *S. elaeagnifolium*. This field was the third nearest to *S. elaeagnifolium* and the first to develop above ground potato foliage in early August 2007. At least two full generation cycles were completed before the beetles entered diapause (Figure 4). The beetles, however, did not spread from this infested potato field to the neighbouring potato fields.

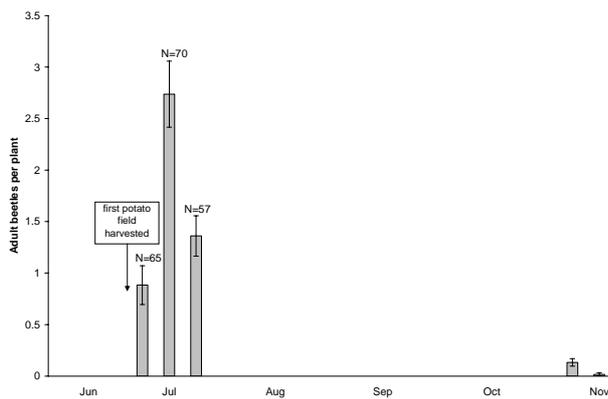


Figure 3: Adult beetles per *S. elaeagnifolium* plant during weekly censuses in the population in Arisvi, Lesvos. Sample size was 60 plants per census unless otherwise stated. Means \pm SE.

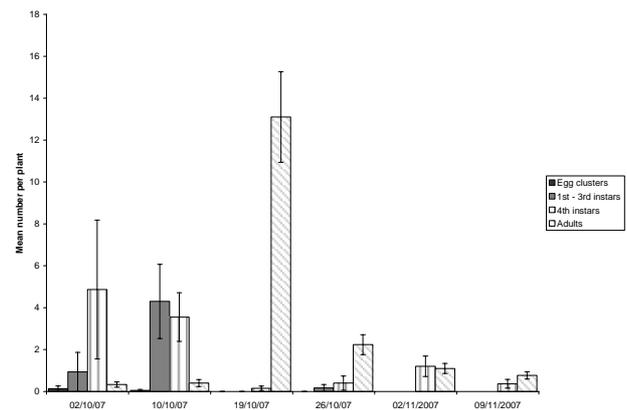


Figure 4: Density of different developmental stages of CPB in the infested summer potato field in Arisvi. Means \pm SE.

4 Discussion

4.1 Distribution of *Solanum elaeagnifolium* in Greece

The results show that *S. elaeagnifolium* has spread since the last distribution map was published by Boratynski (1992). This was expected and is in accord with the plant's spread in other countries of the Mediterranean Basin (Mekki 2007).

4.2 Impact of *Solanum elaeagnifolium* on the native *Glaucium flavum*

We observed significantly lower visitation rates for *G. flavum* in sites where *S. elaeagnifolium* was present compared to sites where *S. elaeagnifolium* was absent. Similarly, Brown *et al.* (2002) found that potted *L. alatum* plants that were arranged in blocks with potted plants of the invasive *L. salicaria* and were exposed to free insect pollination received fewer visits, which resulted in significantly lower seed set than *L. alatum* plants in monospecific treatments. Chittka and Schürkens (2001) showed that in invaded patches the visitation to the native *Stachys palustris* was reduced by 50% and the seed set was reduced by 25% relative to uninvaded patches when the invasive *Impatiens glandulifera* was present. Aigner (2004), however, observed no significant difference in visitation and seed set whether or not the invasives *Carpobrotus* spp. and/or *Cakile maritime* were present alongside the native *Dithyrea maritima*.

In addition, *G. flavum* flowers in invaded sites received more visits from *Xylocopa* spp., and Megachilid bees and fewer from *Amegilla* spp. This can be attributed to *Amegilla* spp.'s apparent preference for *S. elaeagnifolium* flowers, which may be due to their ability to efficiently retrieve the extremely nitrogen and protein-rich pollen typical for *Solanum* flowers (Buchmann 1986) from the poricidal anthers of *S. elaeagnifolium*. Poricidal flowers can only be efficiently harvested by bees which sonicate (buzz) the anthers (Buchmann and Cane 1989) and *Amegilla* spp. are known to be buzz-pollinators (Hogendoorn *et al.* 2007). Almost 75% of all visits to *S. elaeagnifolium* in invaded sites were from *Amegilla* spp., which are the main visitors of *S. elaeagnifolium* on Lesvos (personal observation). *S. elaeagnifolium* therefore may act as a magnet species for *Amegilla* spp. The only other bee species recorded in invaded sites, which are able to sonicate were *Xylocopa violaceous* and *X. iris*. Both showed relatively little interest in *S. elaeagnifolium* flowers, which might be due to their size and weight, and the resulting difficulty to land on *S. elaeagnifolium* flowers.

Our results indicate that the presence of *S. elaeagnifolium* can significantly lower the visitation of *G. flavum*. As *G. flavum* is pollen limited (unpublished data) the lower visitation rate can be expected to eventually lead to a reduction in seed set through fewer conspecific pollen grains arriving on the stigmas, which in turn may impact the abundance of the plant in invaded sites and lead to inbreeding depression.

4.3 *Solanum elaeagnifolium* and potato cultivation

The first occurrence of adult beetles on the stand of *S. elaeagnifolium* in vicinity to spring potato fields in Arisvi coincides with the harvest of the first potato field. This suggests that potato is preferred over *S. elaeagnifolium* and that some beetles moved from the harvested potato fields to the population of *S. elaeagnifolium* in search of alternative food plants. The discrepancy between the large numbers of beetles that infested the potato fields in vicinity of *S. elaeagnifolium* and the relatively small number of beetles found on *S. elaeagnifolium* after harvest implies that most beetles entered diapause and burrowed into the soil after harvest.

Only one out of 10 summer potato fields was infested by CPB. The infested field was the third closest to the population of *S. elaeagnifolium* and the first to develop above-ground potato biomass. Delayed planting is an effective cultural control (Weber and Ferro 1994) as the absence of food can trigger diapause. It could be argued that the early planting of the infested field might have drawn away CPB from the population of *S. elaeagnifolium*. In the absence of recaptured marked beetles this can not be proven, but it is unlikely that beetles unsuccessfully searched for food for four weeks without entering diapause (Horton and Capinera 1988a).

The last beetles on *S. elaeagnifolium* before potato foliage was available in the summer potato field were found in late July, one week before the summer potato field produced the first above ground biomass. Therefore there was a week when CPB was neither found on *S. elaeagnifolium* nor was potato foliage available at the time. It is possible that the planting of the tubers attracted adult CPB or that beetles spend a week searching for food until the above ground potato biomass became available. The summer potato infestation resulted in at least two further generations, which will add to the number of post-diapause beetles in spring. It was not proven that the beetles infesting the summer potato field in Arisvi stemmed from beetles that had previously fed on *S. elaeagnifolium*, but given that the only beetles seen in the study area prior to infestation were recorded on *S. elaeagnifolium*, this is likely. It is therefore probable that the presence of *S. elaeagnifolium* in vicinity of spring and summer potato fields can facilitate the infestation with CPB of summer potato fields.

In November very low densities of CPB were found on *S. elaeagnifolium*. It is likely that these stemmed from infested summer potato fields and were ready to diapause. It has been reported that beetles often move off the potato fields to diapause in field margins (Weber and Ferro 1993).

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