

Manuscript Information	
Journal Acronym	TTPM
Volume and issue	
Author name	
Manuscript No. (if applicable)	_A_366238

International Journal of
(Tropical) Pest Management



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Invasive weed facilitates incidence of Colorado potato beetle on potato crop

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(Received 18 March 2008; final version received 2 December 2008)

We examined whether the invasive silverleaf nightshade, *Solanum elaeagnifolium* (Cavanilles) can facilitate the infestation of potato (*Solanum tuberosum* (L.)) by the Colorado Potato Beetle, CPB, *Leptinotarsa decemlineata* (Say) in Greece, which would have important financial and pest management implications for the growing of potato crops. In laboratory tests, CPB from Lesvos could utilise *S. elaeagnifolium* if supplied with whole plants. In the field, however, CPB was only found on *S. elaeagnifolium* after the start of the spring potato harvest and the resulting loss of potato foliage, and no eggs were laid. This suggests that *S. elaeagnifolium* provides only a temporary food resource for adult beetles. One of 10 surveyed summer potato fields near the study population of *S. elaeagnifolium* was infested with CPB. It is likely that the presence of *S. elaeagnifolium* in the vicinity of spring and summer potato fields can help maintain CPB population viability in the immediate post harvest period of the spring potato crop, which may in turn facilitate the infestation of summer potato fields with CPB.

Keywords: Invasive; alien; Colorado potato beetle; crop pest; *Solanum elaeagnifolium*; *Leptinotarsa decemlineata*; potato; Lesvos; Greece

1. Introduction

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 in many countries for avoiding a major reduction in yield. It is an oligophagous pest that in the wild feeds exclusively on Solanaceae, especially on the genus *Solanum* (Hsiao 1978). In the 1850s, CPB expanded its host range from the principal native hosts *Solanum rostratum* (Dunal) and *S. angustifolium* (Miller) to include potato, *S. tuberosum* (L.) (Casagrande 1985; Hare 1990). Originally native to Mexico, CPB now occurs in much of the USA, Asia and Europe it arrived in Greece in 1963. While CPB found in northern, central, and eastern USA, Europe and Asia feed predominantly on cultivated potatoes, many populations in the southern USA and in Mexico infest native hosts (Hsiao 1978).

It is well documented that populations of CPB 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 1988a; Lu and Logan 1993; Forister et al. 2007).

Hsiao (1978) showed that *S. elaeagnifolium* is not a suitable host for larval growth of CPB from Utah, New Mexico, and Texas. CPB from Arizona, however, developed better on *S. elaeagnifolium* than on

any other plants tested, including potato and *S. rostratum* (Hsiao 1978). It has been observed that, where *S. rostratum* is present in southwestern states, other than Arizona, *S. elaeagnifolium* is rarely attacked by the Colorado potato beetle (Hsiao 1978).

It was previously shown that larvae of CPB from Athens, Greece experience high mortality if fed exclusively on *S. elaeagnifolium* (Hsiao 1981). *Solanum elaeagnifolium* is an invasive, which was first recorded in mainland Greece in Thessaloniki, in the 1920s and on the island of Lesvos in 1975 (Economidou and Yannitsaros 1975). According to the local potato growers the arrival of CPB on the island of Lesvos dates back to approximately 1995. The extended growing season on Lesvos and in 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 second 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, necessitating frequent insecticide applications, the summer crop is generally uninfested. This can be attributed to the lack of alternative food plants between the two crops, because the absence of a suitable host plant can trigger diapause in adult CPB (Horton and Capinera 1988b). 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

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the implications for potato cultivation near populations of *S. elaeagnifolium* have not been investigated. Here, we aim to (i) test whether CPB utilises *S. elaeagnifolium* in laboratory choice and no-choice tests; (ii) identify where and when CPB feeds on wild *S. elaeagnifolium* on Lesvos, Greece; and (iii) assess whether *S. elaeagnifolium* can facilitate CPB infestation of the summer potato crop by acting as a stepping-stone host.

2. Methods

2.1. Life history of *S. elaeagnifolium* and Colorado potato beetle

Solanum elaeagnifolium (silverleaf nightshade) is native to South and Central America and South-western parts of North America. Interest in the plant increased in the 1970s as *S. elaeagnifolium* spread outside its native range. 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 a listed noxious weed in 21 states of the US (Roche 1991) and was recently classified as a weed which requires international measures to stop its spread or contain infestations in Europe and the Mediterranean Basin (EPPO 2004). In Greece *S. elaeagnifolium* is widespread especially on the mainland and locally very abundant (Economidou and Yannitsaros 1975; Boratynski et al. 1992; Tscheulin et al. 2008).

Solanum elaeagnifolium is a branched, deep-rooted, perennial herb, 0.3–1.2 m tall with leaves which are densely and closely tomentose with stellate hairs (El Naggar and Abdel Hafez 2003). It usually grows in places with summer moisture or irrigation (Boyd et al. 1984). *Solanum elaeagnifolium* lowers crop yield through competition (Boyd and Murray 1982b) and the plant's spiny leaves and coarse stems may lower the quality of hay taken from infested fields (Boyd et al. 1984). The fruit and foliage are also toxic to livestock. Cattle that consume 0.1–0.3% of their body weight in ripe berries display poisoning symptoms (Buck et al. 1960), whereas sheep are more resistant to the toxins, and goats are unaffected (Boyd et al. 1984). *Solanum elaeagnifolium* can spread by seed, rhizomes, and/or root fragments (Boyd and Murray 1982a). Individual berries produce 24–149 seeds (Boyd and Murray 1982b), which can add up to 5–100 million seeds per acre (Cooley and Smith 1971). Seeds may be dispersed by water, machinery, agricultural products or animal faeces; studies indicate that 10% of seed is still viable after passing through the gut of sheep (Boyd et al. 1984). Dried plants may also uproot and disperse by wind, like tumbleweeds, spreading seed along the way (Boyd et al. 1984).

In Greece, the annual cycle of CPB begins with the emergence from diapause in early spring (February to March). Beetles then disperse to potato fields where they will feed and subsequently start oviposition. Females lay up to 2000 eggs in clusters of 10–30, on the undersides of the potato leaves. Eggs hatch in 4–12 days depending on ambient temperature and humidity. Larvae moult four times during the following 2–3 weeks after which they pupate. Pupa-tion lasts 5–15 days and occurs in the soil, after emergence adults either lay eggs or enter diapause, depending on environmental conditions (personal observations).

2.2. Establishment of CPB culture

Sixty adults that had freshly emerged from diapause at the time of collection in April 2007 served as the founder population of the laboratory culture. They were taken from a population in Arisvi, Lesvos on potato (39°13'57.46"N, 26°13'18.18"E). The area around the collection site consists mainly of cultivated land in which potato, olive and grape production is dominant. The closest population of *S. elaeagnifolium* (39°14'8.44"N, 26°13'30.58"E) is less than 0.5 km away from the collection site and contained 475 individuals/shoots. There, it grows mainly on road verges and along field margins.

The collected beetles and the resulting offspring were maintained continuously on potted potato plants (variety 'Spunta') grown from tubers in mesh cages that were placed outside. Pre-pupal larvae were transferred to plastic buckets with soil for pupation. All beetles used in the experiments were from the F₂ generation of the initial stock. All plants were grown in standard greenhouse medium under identical conditions of light, temperature and fertilization. *Solanum elaeagnifolium* plants were grown from seeds collected in Skala Eresou (39°08'22.02"N, 25°55'20.31"E) in 2006. The experiments were conducted under a 15-h photophase and at a temperature of 25 ± 3°C. These conditions were determined suitable for growth in preliminary experiments.

Voucher specimens from the founder individuals were placed in our collection, the 'Melissotheque of the Aegean' (Petanidou and Lamborn 2005).

2.3. Host plant affinity experiments

Host plant affinity was tested in no-choice tests (these involved providing the beetles with only one or the other plant) under two experimental situations: in Petri dishes providing single leaves and in cages providing whole plants. Host plant affinity tests in Petri dishes allow a high number of replicates due to their minimal space requirements. However, the conditions in Petri dishes are more artificial than in cages, which is why we chose to carry out no-choice

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tests in cages as well. For both experiments, the F₂ generation of post-diapause field collected adults was reared on two solanaceous plants, *S. elaeagnifolium* and *S. tuberosum*.

For the Petri dish experiments, F1 CPB females were left to oviposit on caged potato plants and the eggs were detached from the leaves and placed in separate Petri dishes on moistened filter paper. After hatching, beetle larvae were counted, assigned to individual Petri dishes lined with moistened filter paper, and fed on foliage from potted plants of *S. elaeagnifolium* or *S. tuberosum*. This procedure ensured that neonate larvae were not preconditioned by feeding on potato or *S. elaeagnifolium* prior to the host acceptability tests, which would have biased the results of the feeding trials (Cuda et al. 2002). Sixty Petri dishes were set up with individual larvae fed on *S. elaeagnifolium* and 60 with individual larvae fed on potato foliage. Plant foliage was replaced daily and any deaths, the time of death and developmental times per larval stage were noted. After emergence from pupation the adults' live and dry weight was recorded. Developmental times, survival and adult weight are measures of host acceptance (Hsiao 1978). Beetles that had not emerged as adults after 50 days were considered dead, in which case we assumed an age of 29 days at time of death, which was the average developmental time for CPB larvae fed on potato foliage in this experiment. We followed this procedure as it was not possible to assess whether a pupa was dead or alive due to the experimental set-up. Survival distribution curves for CPB larvae on the two host plants were generated by the Kaplan–Meier method (Kaplan and Meier 1958) and compared using the Breslow test (Breslow 1970) as a test of equality of the survival distributions.

A choice test using mated females was conducted to measure the feeding preference of female adult CPB for the two plants. Single females were placed in the centre of a Petri dish, and two leaf discs of 21 mm diameter, one of each plant, punched from mature leaves, were provided at opposite ends. Each choice test was run for 180 min and every 30 min the percentage leaf area eaten was estimated at a resolution of 5% leaf area. Sixty replicates with different females were conducted. Additionally, 20 leaf discs of each plant were desiccated in an oven to assess their dry weight. Dry biomass of *S. elaeagnifolium* leaf discs was 33.4 ± 1.40 mg ($n = 20$) and dry biomass of potato leaf discs was 18.25 ± 0.41 mg ($n = 20$). The average dry weights of the discs were used to calculate the biomass consumed in the choice test from the percentage leaf area eaten (Forister et al. 2007). As the data were not normally distributed, separate Wilcoxon sign ranked tests were used to compare the net consumed biomass per food plant at each time interval.

For the cage experiments, beetle larvae were counted after hatching, assigned to cages and fed on potted plants of *S. elaeagnifolium* and *S. tuberosum*. The cages were made of a thin wooden frame (0.30 × 0.38 × 0.88 m) on which we stapled a fine mesh. The cages were placed on individual plastic trays. We used six cages per plant species with each containing one potted host plant and 10 beetle larvae as one plant can support the full development of at least 10 beetles without complete defoliation (personal observation). Prepupae were placed individually into glass vials with moist soil for pupation. At the end of the experiment we counted the number of emerged beetles. A Mann–Whitney *U*-test was used to compare the number of emerged adults from both treatments.

2.4. Field experiments for CPB on *S. elaeagnifolium* and potato

2.4.1. Mark and recapture

In order to investigate whether CPB populations feeding on spring potato foliage utilize *S. elaeagnifolium* after potato harvest, we marked a total of 300 CPB beetles and released them in potato fields at various distances from the nearest population of *S. elaeagnifolium* in Arisvi. The beetles were marked with colour-coded, round labels of 0.9 mm diameter that were attached to the beetles' pronotum with superglue (Piper 2003). Fifty marked beetles each were released within potato fields at 10, 25, 40, 55, 80 and 450 m distance in random directions from the population of *S. elaeagnifolium* in early June 2007, 2 weeks before the potatoes were harvested. The population of *S. elaeagnifolium* was surveyed once a week throughout summer and autumn (from June to November) for marked beetles by searching a minimum of 20 randomly chosen plants per survey.

2.4.2. Assessment of CPB densities on *S. elaeagnifolium*

The densities of CPB on *S. elaeagnifolium* were assessed periodically from May to November in Arisvi to evaluate whether there is a possibility of *S. elaeagnifolium* acting as an alternative host plant for CPB in the wild. Additionally, the herbivore damage caused by CPB on *S. elaeagnifolium* was assessed to determine whether CPB feeds long enough on *S. elaeagnifolium* to bridge the time interval between the two potato crops. During the surveys for herbivore damage we also searched the plants for egg clusters of CPB. For the weekly CPB density and herbivore damage surveys a minimum of 36 *S. elaeagnifolium* plants was chosen randomly for each survey. As *S. elaeagnifolium* is deep-rooted and can reproduce vegetatively we could not distinguish between ramets and individual plants. We therefore determined the

total abundance of *S. elaeagnifolium* by considering branches that grew within 15 cm from each other as one plant. All *S. elaeagnifolium* plants in the population were counted.

2.4.3. Assessment of CPB densities on the summer potato crop

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 from the nearest population of *S. elaeagnifolium* were 380, 500, 660, 2000, 4500, 4600, 4700, 4750, 5400 and 5600 m. 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.

2.5. Statistical analyses

All analyses were carried out using the statistical software SPSS 14.0.0 (SPSS Inc. 1989–2005). Throughout the manuscript means are followed by SE.

3. Results

3.1. Host plant affinity experiments

In the Petri dish host plant affinity experiment, the survival distributions of 60 individual CPB fed on *S. elaeagnifolium* and 60 individual CPB fed on

potato were significantly different ($\chi^2_{1,119} = 99.9$, $P < 0.001$; Figure 1). Larval CPB on *S. elaeagnifolium* had a survival rate to adulthood of only 1.7% while 76.7% of the CPB larvae on potato reached adulthood. The average age at death was 5.8 ± 3.8 days for larvae on *S. elaeagnifolium* and 16.7 ± 7.9 days for larvae on potato ($Z_{1,72} = -5.048$, $P < 0.001$). Given the low survival rate of larvae on *S. elaeagnifolium*, developmental times and adult weights were not compared between treatments.

During the choice tests, 41 of the 60 beetles in Petri dishes consumed at least 5% of either one or the other plant discs and the data from the 19 non-feeding beetles were discarded. Only the feeding data at 30, 60, 90 and 120 min were analysed, as by 150 and 180 min some beetles had eaten entire leaf discs, which would have biased the results. Beetles consumed on average more potato foliage than *S. elaeagnifolium* foliage (Figure 2) but the net leaf biomass eaten was not significantly different at any time interval ($P > 0.05$ in all cases).

In the cage host plant affinity experiment, of the originally 10 first instar larvae per cage a mean of 3.5 ± 0.89 and 1.5 ± 0.5 adults emerged from larvae fed on *S. elaeagnifolium* and potato plants, respectively. The difference was not significant ($Z_{1,11} = -1.702$, $P = 0.092$). On *S. elaeagnifolium* the CPB larvae fed exclusively on flowers until the end of the second instar stage and from the third instar onward also leaves were eaten. On potato, larvae fed on foliage throughout their development. It was observed that larvae fell off the food plants in both treatments and subsequently died.

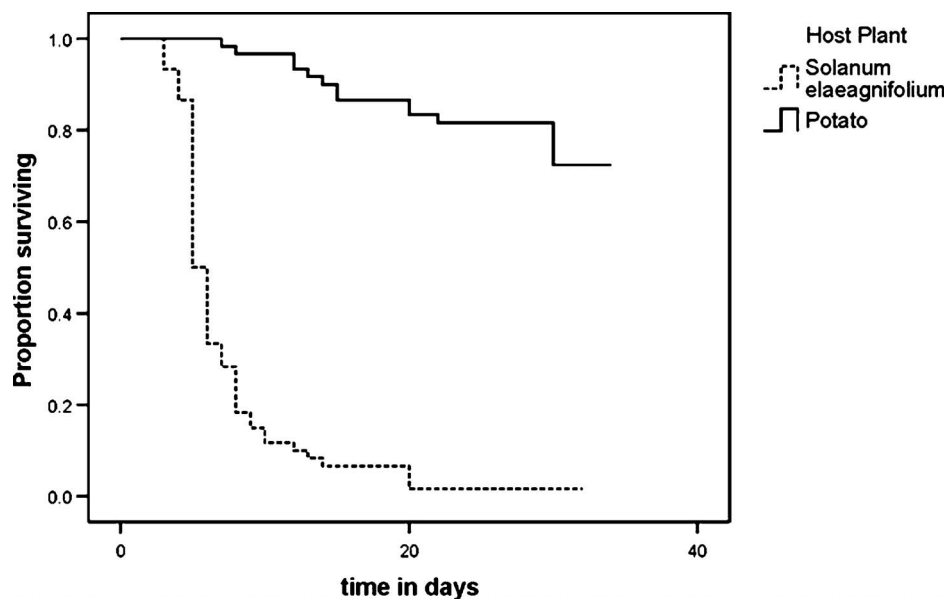


Figure 1. Survival of 60 individuals (first instar larvae at time 0) fed on foliage of *Solanum elaeagnifolium* and 60 individuals fed on potato foliage in individual Petri dishes.

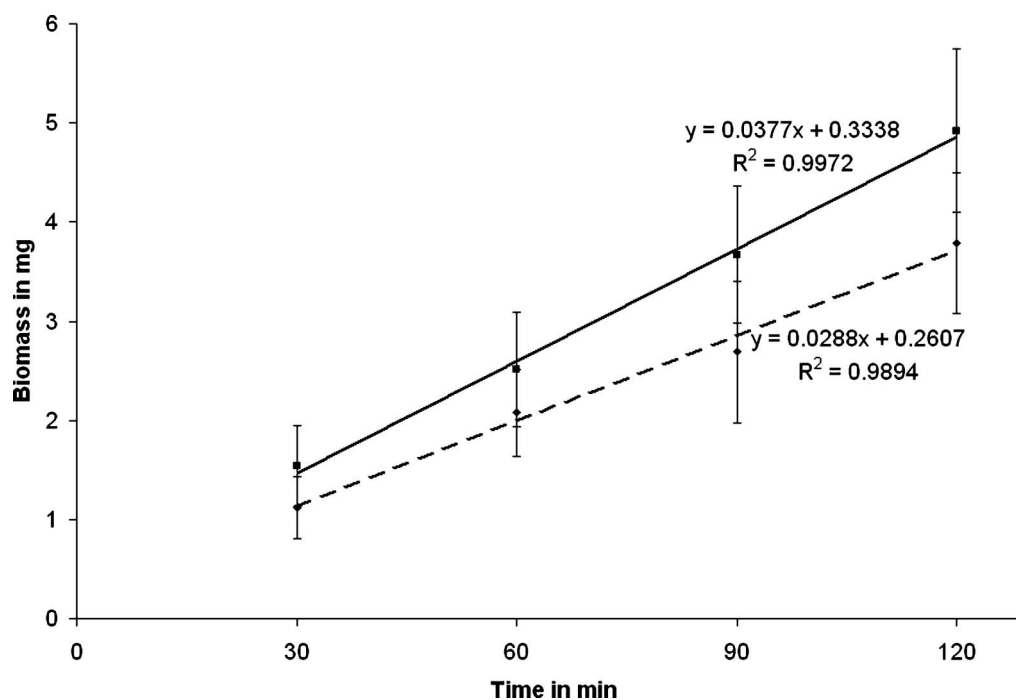


Figure 2. Leaf biomass eaten by female adult CPB during a 120-min feeding trial offering the choice between leaf discs of *S. elaeagnifolium* (e) and potato ("). Values are means \pm SE. Regression lines are presented for CPB feeding on *S. elaeagnifolium* (dashed line) and potato (solid line). Measurements of goodness-of-fit are given within the figure.

3.2. Field experiments for CPB on *S. elaeagnifolium* and potato

3.2.1. Mark and recapture

Beetle movement after potato harvest was not observed, and none of the 300 previously marked beetles was recaptured on the population of *S. elaeagnifolium* in Arisvi during the weekly surveys between early June and mid November.

3.2.2. Assessment of CPB densities on *S. elaeagnifolium*

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 2 weeks of harvest the number of CPB on *S. elaeagnifolium* continued to rise. In mid July, when all of the fields within 500 m 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*. The total *S. elaeagnifolium* abundance in the surveyed population in Arisvi was 475 shoots on 164 m² or 2.9 plants/m². It was observed that on *S. elaeagnifolium* only flowers (corollae, androecia and gynoecia) were eaten by CPB. The proportion of *S. elaeagnifolium* flowers damaged and

time of damage is consistent with changes in beetle density (Figure 4). No eggs were deposited on *S. elaeagnifolium* throughout the observation period from June to November.

3.2.3. Assessment of CPB densities on the summer potato crop

CPB was only found in one field on the summer potato crop at a distance of 660 m 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 beetles entered diapause (Figure 5). CPB, however, did not spread from this infested potato field to the neighbouring potato fields.

4. Discussion

4.1. Host Plant affinity in the laboratory

Significantly fewer larvae survived to adulthood if fed on *S. elaeagnifolium* rather than potato foliage. This implies that potato is a superior host plant for CPB. As host affinity is known to be heritable (Lu and Logan 1993; Forister et al. 2007) and as *S. elaeagnifolium* is the main food plant in some populations of CPB (Hsiao 1978, 1981) it seems surprising that the Lesvos population of beetles has not yet included this solanaceous plant in their host range, considering that both plant and beetle have

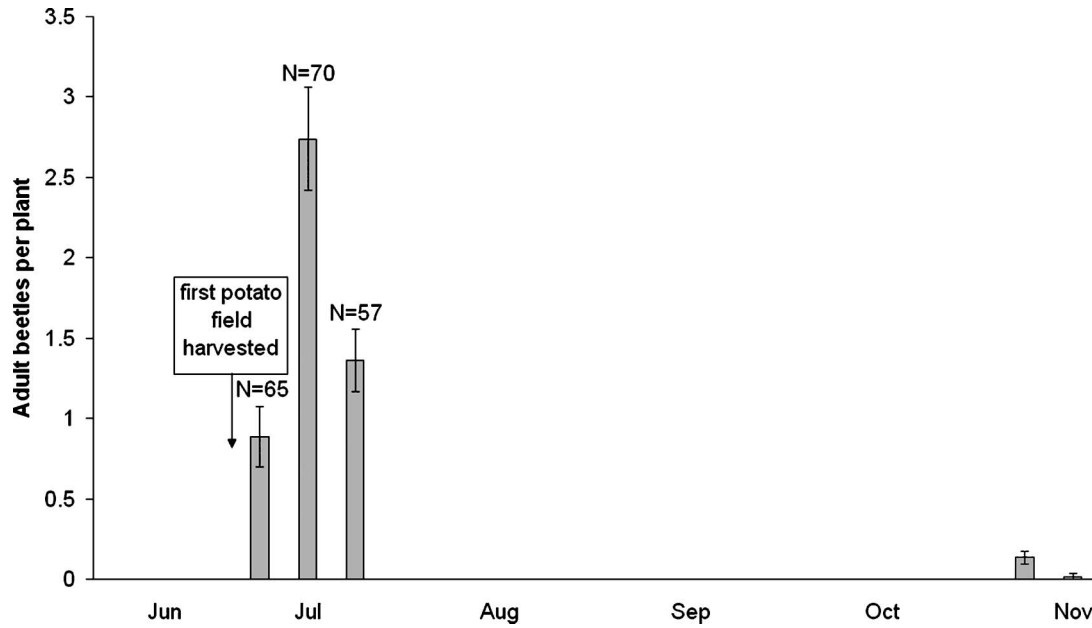


Figure 3. Adult beetles per *S. elaeagnifolium* plant during weekly censuses in the population in Arisvi, Lesvos. Sample size was 60 plants per census unless otherwise stated.

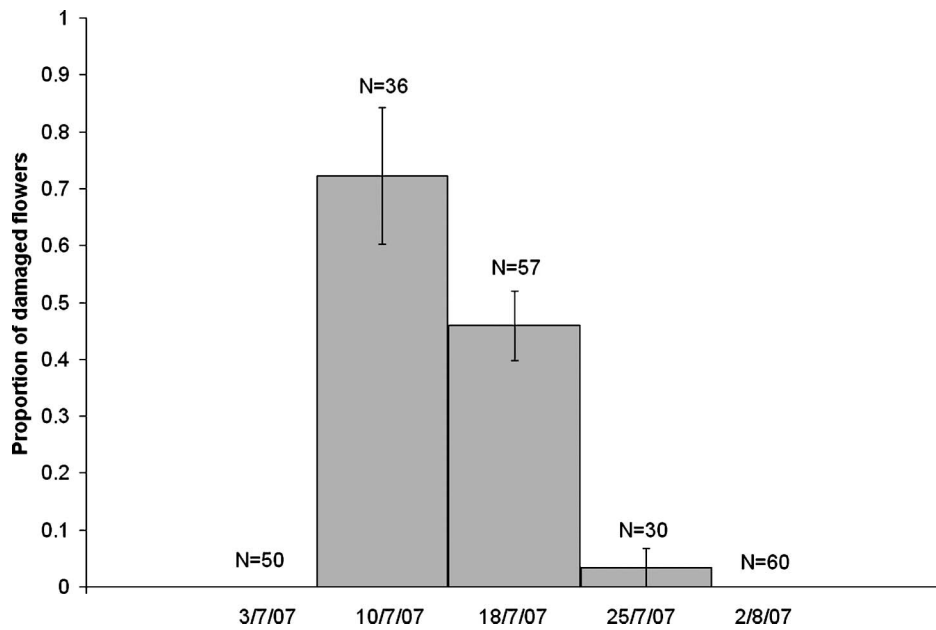


Figure 4. Proportion of *S. elaeagnifolium* flowers damaged by CPB in Arisvi.

been sympatric for more than a decade in the absence of *S. rostratum*, and that the beetles are known to readily adapt (Hare and Kennedy 1986; Hsiao 1988). The finding that *S. elaeagnifolium* foliage is unsuitable larval diet is in accordance with Hsiao (1981), who investigated the larval development of CPB collected from a population in Athens, Greece. This study, however, was carried out before *S. elaeagnifolium* became invasive in Greece. It can therefore be assumed that the beetle population examined had not

been in contact with *S. elaeagnifolium*. Hsiao (1978) also found that *S. elaeagnifolium* was not a suitable host for CPB from Utah, New Mexico and Texas, however, the ancestral host *S. rostratum* was predominant in this situation.

Larval development of insects on different food plants in the laboratory may or may not be comparable to larval development in the field (Wade 1994; Forister et al. 2007). In our study, as well as in previous studies (Hsiao 1978, 1981; Lu and

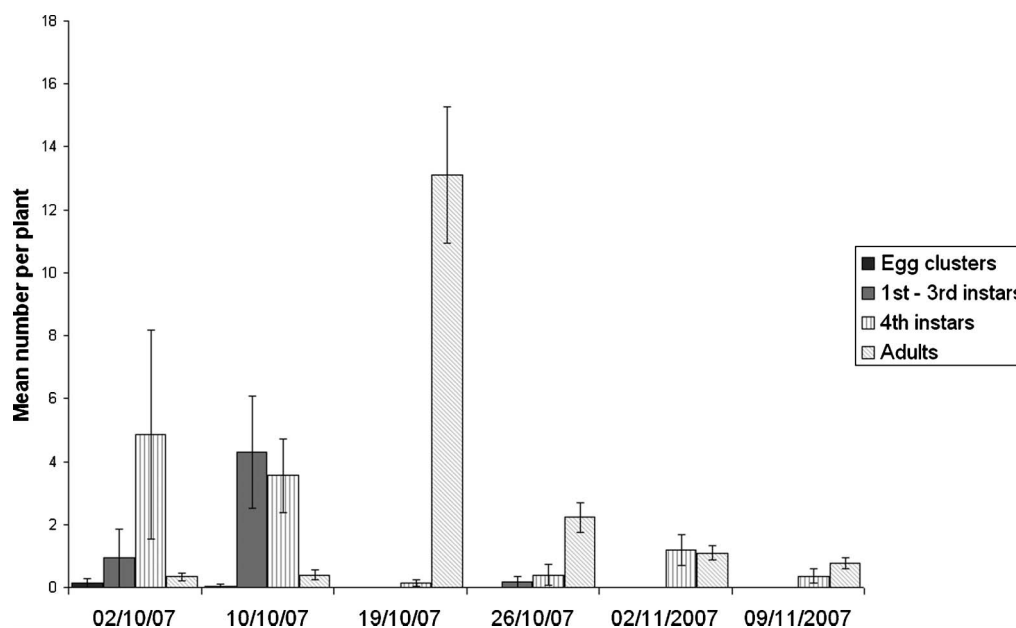


Figure 5. Density of different developmental stages of CPB in the infested summer potato field in Arisvi.

Logan 1994; Forister et al. 2007), fresh foliage was offered. We observed that first and second instar larvae exclusively fed on flowers in the experiment using caged and potted plants, which resulted in survival rates that were not significantly different from survival rates on potted potato plants. It is, therefore, likely that first and second instar larvae are unable to utilize *S. elaeagnifolium* foliage, which could have led to the high mortality observed when providing only foliage. Potato contains on average six times more glycoalkaloid (solanine, tomatine, and atropine) than *S. elaeagnifolium* (Harrison and Mitchell 1988), which suggests that the high larval mortality is not due to the plant's chemical defenses. It may be that first and second instar larvae cannot utilize foliage due to the leaves being densely and closely tomentose with stellate hairs. This form of physical defence may be particularly effective against small insect herbivores.

Contrary to the results for larval development on foliage in Petri dishes, we did not find a significant difference between the number of emerging adults from larvae feeding on whole potted plants of potato and *S. elaeagnifolium*. However, given the small sample size (six replicates per treatment) this result should be treated with caution. The proportion of emerged adults per initial first instar larvae on potted whole *S. elaeagnifolium*, compared to foliage in Petri dishes, does, however, represent a more than 20-fold increase. Given also the fact that first and second instar larvae fed exclusively on flower parts, this suggests that foliage is indeed unsuitable food source for first and second instar larvae. Previous studies on the host affinity of CPB for *S. elaeagnifolium* in which only foliage instead of whole plants containing

flowers was offered (Hsiao 1978, 1981; Lu and Logan 1994; Forister et al. 2007) might have overestimated larval mortality. Flowers might be more palatable than foliage as they lack the stellate hairs (El Naggar and Abdel Hafez 2003).

Many larvae fell off the food plant in both treatments and subsequently died. It is likely that in the field larvae would have been able to find and climb up the same or a different food plant. As this was not possible due to the experimental setup (and smooth plastic flower pots used) the mortality rate might have been overestimated, although falling off might also cause a certain level of mortality through ground predators in the field.

Beetles consumed on average more potato foliage than *S. elaeagnifolium* foliage, but the difference was not significant at any time interval. This shows that mated female beetles from Arisvi readily accept *S. elaeagnifolium* foliage. Hsiao (1978) reported considerable variation in the utilization of *S. elaeagnifolium* across different populations of CPB. In this study, however, host plant suitability in adults was measured in terms of reproduction and no choice of host plant was given. Mated female beetles from New Mexico and Texas entered diapause without laying eggs when fed on *S. elaeagnifolium* foliage, while Arizonan beetles showed normal egg laying activity and high fecundity (Hsiao 1978). However we were unable to test if the consumption of *S. elaeagnifolium* influences diapause behaviour.

4.2. Host plant affinity in the wild

The first occurrence of adult beetles on the population of *S. elaeagnifolium* in the vicinity of 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 food plants. The discrepancy between the large total number of beetles that infested the potato fields in the vicinity of *S. elaeagnifolium* and the relatively small number of beetles found on *S. elaeagnifolium* after harvest indicates that most beetles entered diapause and burrowed into the soil after harvest. This could explain why none of the marked beetles was recaptured on *S. elaeagnifolium*. Hsiao (1978) showed that the proportion of non-adapted female beetles laying eggs on *S. elaeagnifolium* rather than entering diapause is especially low if larvae were raised on potato. As no beetles were found on *S. elaeagnifolium* prior to potato harvest, all adults recorded on *S. elaeagnifolium* after harvest must have completed their larval development on potato. This could explain why no egg clusters were found on *S. elaeagnifolium*.

In November very low densities of CPB were found on *S. elaeagnifolium*. It is likely that these derived from infested summer potato fields and had left the latter after the potato harvest either in search for food or a place to diapause. It has been reported that beetles often move off the potato fields to diapause in field margins (Weber and Ferro 1993).

Only one in 10 of 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 4 weeks without entering diapause (Horton and Capinera 1988b). The last beetles on *S. elaeagnifolium* before potato foliage was available in the summer potato field were found in late July, 1 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 potentially add to the number of post-diapause beetles in spring.

5. Conclusion

CPB from Arisvi, Lesvos, could utilise *S. elaeagnifolium* and undergo a full cycle from first instar larva to adult in the laboratory if given the choice of food plant parts. During first and second larval instars the larvae fed exclusively on flower parts. From third instar onwards also leaves were eaten. In the field, CPB was only found on *S. elaeagnifolium* after the first potato fields had been harvested, which suggests that potato is preferred over *S. elaeagnifolium*. Adult *L. decemlineata* females readily accepted *S. elaeagnifolium* in the laboratory, however, female CPB did not lay any eggs on *S. elaeagnifolium* in the field. *S. elaeagnifolium* can therefore only constitute a temporary food plant. 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 likely that the presence of *S. elaeagnifolium* in vicinity of spring and summer potato fields facilitates the infestation with CPB of summer potato fields. Further research is needed to determine whether the economical benefit would justify a control programme against *S. elaeagnifolium* near potato cultivations.

If the overall benefit (e.g. higher yield, fewer pesticide applications) outweighs the management effort (i.e. cost of weed control) actions towards eradicating an invasive are economically viable (Fraser et al. 2006). As complete eradication using pesticides has proven difficult so far (Eleftherohorinos et al. 1993; Baye et al. 2007) biological control of *S. elaeagnifolium* in the Mediterranean Basin has been suggested (Sforza and Jones 2007). Biological control of this weed has been successfully established in South Africa using two leaf-feeding chrysomelid beetles (Hoffmann et al. 1998) and might be able to reverse potential yield losses, which are due to the presence of *S. elaeagnifolium* near potato cultivations.

Acknowledgements

This research project is co-financed by the EU-European Social Fund (80%) and the Greek Ministry of Development-GSRT (20%). Additional funding was contributed by the Helmholtz Centre for Environmental Research – UFZ. We thank Ioannis Bazos for help with locating the *Solanum elaeagnifolium* populations on Lesvos.

References

- Baye Y, Ameur A, Bouhaches M, Taleb A. 2007. Strategy for the chemical control of *Solanum elaeagnifolium* Cav. in Morocco. EPPO Bull. 37(1):145–152.
- Boratynski A, Browicz K, Zielinski J. 1992. Chorology of trees and shrubs in Greece. Poznan/Kornik: Polish Academy of Sciences, Sorus.
- Bouhache M, Tanji A. 1985. Assessment of the stock of *Solanum elaeagnifolium* Cav. Yellow Nightshade seeds in the soil of the Tadla (Morocco). Weed Res. 25(1):11–14.

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- Boyd JW, Murray DS. 1982a. Growth and development of Silverleaf Nightshade (*Solanum elaeagnifolium*). Weed Sci. 30(3):238–243.
- Boyd JW, Murray DS. 1982b. Effects of shade on Silverleaf Nightshade (*Solanum elaeagnifolium*). Weed Sci. 30(3):264–269.
- Boyd JW, Murray DS, Tyrl RJ. 1984. Silverleaf Nightshade, *Solanum elaeagnifolium*, origin, distribution, and relation to man. Econ Bot. 38(2):210–217.
- Breslow N. 1970. A generalized Kruskal–Wallis test for comparing K samples subject to unequal pattern of censorship. Biometrika. 57:579–594.
- Buck WB, Dollahite JW, Allen TJ. 1960. *Solanum elaeagnifolium*, silver-leafed nightshade, poisoning in livestock. J Am Vet Med Assoc. 137:348–351.
- Casagrande R. 1985. The 'Iowa' potato beetle, its discovery and spread to potatoes. Bull Entomol Soc Am. 31:27–29.
- Cooley AW, Smith DT. 1971. Silverleaf Nightshade (Whiteweed) establishment from seed and clipped seedlings. Progress Report of Texas A&M University, Texas Agricultural Experiment Station. PR-3198.
- Cuda JP, Parker PE, Coon BR, Vasquez FE, Harrison JM. 2002. Evaluation of exotic *Solanum* spp. (Solanales: Solanaceae) in Florida as host plants for the leaf beetles *Leptinotarsa defecta* and *L. texana* (Coleoptera: Chrysomelidae). Florida Entomol. 85(4):599–610.
- De Wilde J, Hsiao TH. 1981. Geographic diversity of the Colorado potato beetle and its infestation in Eurasia. In: Advances in potato pest management. Stroudsburg (PA): Hutchinson & Ross. p. 47–68.
- Economidou E, Yannitsaros A. 1975. Recherches sur la flore adventice de Grèce. V. Distribution et écologie de *Solanum elaeagnifolium* Cav. Revue de Biologie et d'Ecologie Méditerranéenne. 2(4):29–44.
- El Naggar SM, Abdel Hafez S II. 2003. Leaf surface, pollen morphology, fungal biodiversity and leaf spots of some wild plants in Sinai, Egypt. Feddes Repertorium. 114(1–2):74–90.
- Eleftherohorinos IG, Bell CE, Kotoula-Syka E. 1993. Silverleaf Nightshade (*Solanum elaeagnifolium*) control with foliar herbicides. Weed Technol. 7(4):808–811.
- EPPO. 2004. Invasive alien plants in the EPPO region. European and Mediterranean Plant. Protection Organization (EPPO) reporting service. EPPO panel on invasive alien species.
- Forister ML, Ehmer AG, Futuyama DJ. 2007. The genetic architecture of a niche: variation and covariation in host use traits in the Colorado potato beetle. J Evol Biol. 20(3):985–996.
- Fraser RW, Cook DC, Mumford JD, Wilby A, Waage JK. 2006. Managing outbreaks of invasive species: eradication versus suppression. Int J Pest Manage. 52(4):261–268.
- Hare JD. 1990. Ecology and management of the Colorado potato beetle. Annu Rev Entomol. 35(1):81–100.
- Hare JD, Kennedy GG. 1986. Genetic variation in plant-insect associations: survival of *Leptinotarsa decemlineata* populations on *Solanum carolinense*. Evolution. 40:1031–1043.
- Harrison GD, Mitchell BK. 1988. Host-plant acceptance by geographic populations of the Colorado potato beetle, *Leptinotarsa decemlineata* – role of solanaceous alkaloids as sensory deterrents. J Chem Ecol. 14(3):777–788.
- Hoffmann JH, Moran VC, Impson FAC. 1998. Promising results from the first biological control programme against a solanaceous weed (*Solanum elaeagnifolium*). Agric Ecosyst Environ. 70(2–3):145–150.
- Horton DR, Capinera JL. 1988a. Local differences in host use by two populations of the Colorado potato beetle. Ecology. 69(3):823–831.
- Horton DR, Capinera JL. 1988b. Effects of host availability on diapause and voltinism in a non-agricultural population of Colorado potato beetle (Coleoptera: Chrysomelidae). J Kans Entomol Soc. 61(1):62–67.
- Hsiao TH. 1978. Host-plant adaptations among geographic populations of the Colorado potato beetle. Entomol Exp Appl. 24:237–247.
- Hsiao TH. 1981. Ecophysiological adaptation among geographic populations of the Colorado potato beetle in North America. In: Advances in potato pest management. Stroudsburg (PA): Hutchinson & Ross. p. 69–85.
- Hsiao TH. 1982. Geographic variation and host adaptation of the Colorado potato beetle. In: Proceedings, Fifth International Symposium of Insect-Plant Relationships Wageningen (the Netherlands): Pudocp. p. 315–324.
- Hsiao TH. Ecophysiological and genetic aspects of geographic variations of the Colorado potato beetle. In: Ferro DN, Voss RH, editors. Symposium on the Colorado potato beetle, XVIIth International Congress of Entomology, Amherst, Massachusetts.
- Hsiao TH. 1988. Host specificity, seasonality and biometrics of *Leptinotarsa* beetles. In: Biology of chrysomelidae. Dordrecht: Kluwer. p. 581–599.
- Kaplan EL, Meier P. 1958. Nonparametric estimation from incomplete observations. J Am Stat Assoc. 53:457–481.
- Lu W, Logan P. 1994. Geographic variation in larval feeding acceptance and performance of *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae). Ann Soc Am. 87(4):460–469.
- Lu WH, Logan P. 1993. Induction of feeding on potato in Mexican *Leptinotarsa decemlineata* (Coleoptera, Chrysomelidae). Environ Entomol. 22(4):759–765.
- Mekki M. 2007. Biology, distribution and impacts of Silverleaf Nightshade (*Solanum elaeagnifolium* Cav.). EPPO Bull. 37(1):114–118.
- Petanidou T, Lamborn E. 2005. A land for flowers and bees: studying pollination ecology in Mediterranean communities. Plant Biosys. 139(3):279–294.
- Piper RW. 2003. A novel technique for the individual marking of smaller insects. Entomol Exp Appl. 106(2):155–157.
- Roche C. 1991. Silverleaf Nightshade (*Solanum elaeagnifolium* Cav.). Pacific Northwest Extension Publication. 365.
- Sforza R, Jones WA. 2007. Potential for classical biocontrol of silverleaf nightshade in the Mediterranean Basin. EPPO Bull. 37(1):156–162.
- Tscheulin T, Petanidou T, Zografou C, Pantelis K. Invading the Mediterranean: study of *Solanum elaeagnifolium*, a successful invasive plant from C. America. Earth Conference; University of the Aegean, Mithilini.
- Wade MJ. 1994. The biology of the imported willow leaf beetle, *Plagioderia versicolora* (Laicharting). In: Novel aspects of the biology of the chrysomelidae. Dordrecht: Kluwer Academic. p. 541–547.
- Weber DC. 2003. Colorado beetle: pest on the move. Pesticide Outlook. 14(6):256–259.
- Weber DC, Ferro DN. 1993. Distribution of overwintering Colorado potato beetle in and near Massachusetts potato fields. Entomol Exp Appl. 66:191–196.
- Weber DC, Ferro DN. 1994. Colorado potato beetle: diverse life history poses challenge to management. In: Advances in potato pest biology and management. St Paul: APS Press. p. 54–70.