

Light conditions affect the performance of *Yponomeuta evonymellus* on its native host *Prunus padus* and the alien *Prunus serotina*

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Abstract

The bird cherry ermine moth, *Yponomeuta evonymellus* L., is considered an obligatory monophagous insect pest that feeds only on native European *Prunus padus* L. In recent years, however, increased larval feeding on alien *P. serotina* Ehrh. has been observed. In both species, general defoliation is extensive for shade grown trees, whereas it is high in *P. padus*, but very low in *P. serotina*, when trees are grown in full light conditions. The aim of the present study was to identify how the plant host species and light conditions affect the performance of *Y. evonymellus*. The influence of host species and light condition on their growth and development, characterized by the parameters of pupation, adult eclosion, body mass, potential fecundity, and wing size, was measured in a 2 × 2 experimental design (two light treatments, two hosts). In comparison with high light (HL) conditions, a greater percentage of pupation and a longer period and less dynamic adult emerge was observed under low light (LL) conditions. The effect of host species on these parameters was not significant. In contrast, mass, fecundity and all of the studied wing parameters were higher in larvae that grazed on *P. padus* than on *P. serotina*. Similarly the same parameters were also higher on shrubs in HL as compared with those grown under LL conditions. In general, light conditions, rather than plant species, were more often and to a greater extent, responsible for differences in the observed parameters of insect development and potential fecundity.

Keywords: folivorous insect, high light condition, invasive species, Lepidoptera, low light condition, Yponomeutidae

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Introduction

Research on the relationship between herbivores and their host plants generally focuses on the factors determining host

species choice, and to a lesser extent, on herbivores' preferences and performance within a species. Differences between and within host species can affect trophic levels (Price *et al.*, 1980), such as herbivorous insects, by contributing to differences in the quality of food and to the quality of the conditions that affect the development and reproduction of the herbivores (Alonso & Herrera, 1996; Giertych *et al.*, 2007; Anderson *et al.*, 2013). There are many plant features, such as morphology and anatomy (Calixto *et al.*, 2015; Łukowski

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et al., 2015), as well as chemical composition (Barber & Marquis, 2011; Karolewski *et al.*, 2013), that can affect plant-herbivore interactions. Plants are also strongly influenced by environmental factors (light conditions, humidity, etc.) that affect their physiology and development (Abrams *et al.*, 1992; Barber & Marquis, 2011; Bielinis & Robakowski, 2015).

Forests are complex ecosystems and are typically composed of a number of different niches and specialized microhabitats (Winter & Möller, 2008). Conditions such as canopy density and gaps, forest edges, presence of road, etc., create a specific light conditions in both tropical and temperate forests (Leather & Mackenzie, 1994; Mooney & Niesenbaum, 2012). Shrubs of *Prunus* L., and other understory species, have evolved the ability to grow in a variety of light conditions and possess a range of physiological responses that enable them to adapt to different levels of light (Abrams *et al.*, 1992). Understory plants are an important source of food for herbivores, including folivorous insects (Menken *et al.*, 1992). However, their utility as a food source for folivores may vary with the physiological status of the plant, which can in turn be impacted by the level of abiotic stress (DeLucia *et al.*, 2012). Plants that are exposed to different levels of biotic stress, such as insect feeding and fungal pathogens, try to minimize leaf damage through an induction of various chemical and structural defense mechanisms (Giertych *et al.*, 2006; Eyles *et al.*, 2010). Several hypotheses have been proposed to explain the mechanisms by which changes in a complex of environmental factors can alter the production of defense compounds in leaves (Gong & Zhang, 2014). For example, the carbon/nutrient balance hypothesis postulates that the carbon/nitrogen ratio in plants determines which secondary metabolites will be synthesized (Koricheva *et al.*, 1998b). When the plants grow in high light conditions (HL), resulting in high levels of carbon assimilation, the high levels of carbohydrates are used to produce carbon-based defenses metabolites to repel herbivores. It is plausible that the correlation between light conditions and the production of defense compounds is one of the underlying reasons that understory trees and shrubs, which grow in low light conditions (LL), are frequently more heavily attacked by insect herbivores than tree and shrub species growing in HL conditions. Shade leaves, relative to sun leaves, are characterized by a less resistant structure (Abrams *et al.*, 1992) and lower levels of carbon-based defense compounds (Henriksson *et al.*, 2003; Karolewski *et al.*, 2013).

In European forests, the native bird cherry *Prunus padus* L. and the non-native black cherry *P. serotina* Ehrh. are widespread understory plants (Leather, 1996; Godefroid *et al.*, 2005). The native host range of *P. padus* extends from the southern to the northern parts of Europe (Leather, 1996), whereas *P. serotina* is native to northeastern and central areas of the USA and Mexico (Pairen *et al.*, 2010). *Prunus serotina* is a non-native kenophyte in Europe and is a highly invasive species (Chabrierie *et al.*, 2009; Halarewicz, 2011). Leaves of both *Prunus* species are strongly attacked by a variety of polyphagous insect pests, especially by leaf beetle *Gonioctena* species (Coleoptera: Chrysomelidae) (Leather, 1994; Mađerek *et al.*, 2015) and aphids – *Rhopalosiphum padi* (Heteroptera: Aphididae) (Archetti & Leather, 2005; Halarewicz & Gabryś, 2012). Whereas monophagous ermine moth *Yponomeuta evonymellus* L. (Lepidoptera: Yponomeutidae) attacks almost entirely *P. padus* (Leather, 1986; Menken *et al.*, 1992), and only in recent years also finding on the *P. serotina* (Karolewski *et al.*, 2014).

The genus *Yponomeuta* has received great attention from scientific studies as reflected by the abundance of literature that exists pertaining to the ecology of these mono- and oligophagous moths (e.g., Hora & Roessingh, 1999; Javoš *et al.*, 2005; Bakker *et al.*, 2008; Ulenberg, 2009; Parker *et al.*, 2012). Leather (1986), as well as Turner *et al.* (2010), consider *Y. evonymellus* to be an obligatory monophagous species that feeds only on *P. padus*. In recent years, however, an increase in the number of cases of larval feeding on *P. serotina* (see photos in Karolewski *et al.*, 2014) has been observed. In most cases, larvae will feed on leaves of *P. serotina* shrubs when they touch branches of *P. padus*. The movement of larvae from *P. padus* (where they hatch) on to *P. serotina* is often the result of almost complete defoliation of *P. padus* shrubs, and by this a lack of food. One of the main findings of a previous field experiment was the discovery that *Y. evonymellus* moths can survive on *P. serotina*, a new host plant, although it is difficult due to the differences between the phenology of *P. serotina* and *P. padus* (Karolewski *et al.*, 2014). We consider that light conditions can also play an important role in the development and growth of *Y. evonymellus* on *P. serotina*.

The same folivorous species occur on both *P. serotina* and *P. padus*, but the latter host experiences a much greater loss of leaf mass (Karolewski *et al.*, 2013). The amount of damage, however, also depends on light conditions. Damage is extensive in both species when plants are growing in the shade, however under HL conditions, damage is high in *P. padus* and low in *P. serotina* (Karolewski *et al.*, 2013). The strength of chemical defense in both species is not so different (Karolewski *et al.*, 2014; Mađerek *et al.*, 2015). In this case, decisive are not so much differences in the chemistry of leaves, but their structure. Structure of shade leaves is similar in both *Prunus* species. In contrast, sun leaves of *P. serotina* are particularly thick and tough while this is observed to a much lesser extent in *P. padus*. Thus these observations are the result of many interactions between the host plant and light condition on their growth and structure of leaves, and thus on the possibility of insect grazing.

Previous studies (Alonso, 1997; Łukowski *et al.*, 2014) reported that some species in the family Yponomeutidae are more likely to feed in well-lighted places within an individual shrub, such as the south side of the crown, than in the shade or the north side of the crown. These observations are probably due to the fact that larvae feeding on shrubs growing under HL conditions (in higher temperature) have a greater mass and/or faster pupation process which reduces the time of exposure to predators and parasitoids (Sarfraz *et al.*, 2013; Łukowski *et al.*, 2015). At present, the impact of light conditions on *Y. evonymellus* feeding on *P. serotina* shrubs is not yet known.

The objective of the present study was to determine the effect of the two host species, *P. serotina* and *P. padus*, and the light conditions of their growth habitats, on the performance (parameters of growth and development and potential fecundity) of *Y. evonymellus* moths. Although the influence of the host plant species on the insect feeding has been studied, the results of the previous studies did not take into consideration the interaction of the plant species and light conditions. In particular, no convincing and unequivocal results exist pertaining to the influence of light conditions on the host quality and thus the growth and development of folivorous insects (Roberts & Paul, 2006). We know that leaves of the alien *P. serotina* are not as ideal a food source for *Y. evonymellus* as leaves of the native *P. padus*, however, they can be a substitute

(Karolewski *et al.*, 2014). We hypothesized that in HL conditions the larvae grow better on the native host than on the alien host, while there is no such difference in LL conditions. We also hypothesized that no differences in the performance of *Y. evonymellus* would be observed when larvae fed in LL conditions on shrubs of the two species. Larvae of *Y. evonymellus* at an early stage of development were moved from original *P. padus* shrubs to new environments in either LL and HL conditions of *P. serotina* or *P. padus* shrubs. This translocation to new environments enabled us to precisely determine the effect of changes in host plant in each of the lighting conditions, and thus the quality of food, on adult eclosion, pupation dynamic, body mass, fecundity and wing parameters.

Materials and methods

Insect and plant material

The study was conducted on the bird cherry ermine moth, *Y. evonymellus* (Lepidoptera: Yponomeutidae). Several parameters were used: the insects performance, pupation, adult eclosion, body mass, potential fecundity, and wing size to determine the effect of shrub species and light conditions on the growth and development. Two species of understory shrubs, black cherry (*Prunus serotina* non-native species) and bird cherry (*P. padus*; native species), were used as plant material for this study. In the past *P. serotina* used to be intensively planted in the understory, mainly in Scots pine monocultures on sandy soils, by European foresters. *Prunus serotina* has been able to invade Europe due to its lower requirement for water and nutrients as compared with *P. padus* (Ellenberg *et al.*, 1992; Halarewicz, 2011). In addition to its ability to rapidly establish itself within a habitat poor in nutrients and water, it is also relatively resistant to insect damage (Abrams *et al.*, 1992; Karolewski *et al.*, 2010).

The field experiment was carried out on a research site located in the Kobylepole Forest in Poland (Babki Forest District; 52°36'N, 17°06'E). Earlier observations and research in the area of the Kobylepole Forest indicated that both *Prunus* species exhibit an equal occurrence at the selected site. The *Prunus* shrubs were growing under a canopy of *Pinus sylvestris* L., with an admixture of *Quercus robur* L., *Fagus sylvatica* L., *Carpinus betulus* L., and *Ulmus laevis* Pall. Shrubs (3–5 m high) were selected from HL conditions along wide forest roads or in forest gaps, and within LL conditions under a dense forest canopy (approximately 15–30% of full light as measured using an LAI-2200 Plant Canopy Analyzer) (LI-COR Company, USA). Ten similarly sized shrubs per plant species (*P. padus* and *P. serotina*), growing within the specific light conditions (LL and HL), were selected at the site; comprising a total of 40 shrubs for the study.

Experimental design and measurements

We conducted a continuous daily observation of the larval development in nature. On 18 May 2015, a sample of *Y. evonymellus* larvae, which had reached L2 instar on the same day, were transferred from *P. padus* shoots to selected shrubs for the study, which had no ermine moths and other herbivores on them at that time. Eighty sections of shoots with L2 larvae were selected, forty from HL and forty from LL conditions (in total 80 shoots). We selected shoots with similar number of larvae (ca. 50 specimens). The larvae were then transferred to new shrubs of *P. padus* and *P. serotina* (20 sections of shoots

with larvae per shrub species and light conditions), ensuring that similar light conditions were maintained within the new host shrubs. More specifically, L2 larvae obtained from shoots (LL) were placed on new hosts that were also in LL conditions. Similarly, larvae obtained from shrubs growing under HL conditions were placed on new hosts, growing HL conditions. In order to maintain natural conditions for the experiment, larvae were free to move and were not shielded from biotic and abiotic factors. The sampled sections of shoots with larvae were tied by nylon thread to locations on the new shrubs where larvae typically infest. Larvae of *Y. evonymellus* live gregariously and feed together in one or few groups, and finally join together formed a single bunch of cocoons. In this experiment larvae of this species were unprotected from predators and parasites (without artificial mesh). After 25 days, almost all the larvae had pupated and were moved to the laboratory and the time and percentage of adult eclosion were recorded (pupation time appeared not to differ among treatments). Shoots with pupae were placed in 1-liter plastic containers at ambient temperature with ventilation. Ten randomly selected bunch of cocoons from each species and light variant were used to breed females and to determine potential fecundity. The remaining ten shoots were used to obtain other measurements (mass and wing parameters).

In order to determine the potential fecundity, ovaries were isolated from females that were frozen 1 day after eclosion. During the isolation of the ovary, the female was placed on its back and secured to Sylgard elastomer with microentomological pins in a Petri dish filled with Ringer's solution. Each pinned insect was cut along the ventral side of the abdomen using microsurgery scissors. Fat bodies and Malpighian tubules were removed from the abdomen using micro tweezers. The ovipositor was also removed in order to expose and isolate the ovary. Ovaries were stained with a 0.5% solution of Evans blue in physiological saline. The potential fecundity was assessed as the total number of previtellogenic and vitellogenic oocytes in ovaries.

Newly hatched moths were counted every day and were separated and anesthetized in the vapours of ethyl acetate approximately 3 h after hatching for determination of sex and weight. Body mass was measured with a Sartorius CP225D analytical balance (up to 0.01 mg). The experiment concluded when no new moths had eclosed for a period of 1 week. The number of cocoons was also counted, and each cocoon was dissected to determine percentage of adult eclosion (the sole reason for not eclosing appeared to be parasitization). In addition, wings were cut and removed from moths and the length, width, and area of each forewing and hindwing was measured using a high resolution scanner (800 dpi) and WinFolia 2004 software (Regent Instruments Inc., USA). Wing length and width were defined as the longest and widest point on each wing.

Statistical analyses

Analysis of variance (ANOVA) was used to assess the statistical significance of differences between species of *Prunus*, light conditions, sex, and the interaction between these factors, in moth mass, total wing area, forewing and hindwing area, length and width, and female potential fecundity. Because the analyzed variation over time of the same objects (bunch of cocoons), a repeated-measures ANOVA was used to assess the impact of light conditions and *Prunus* species on the

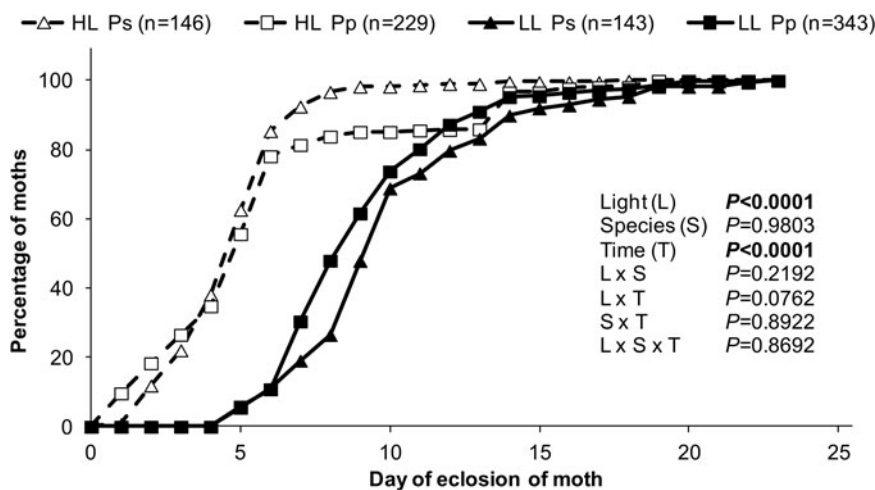


Fig. 1. Cumulative daily percentage of moths that eclosed from pupae derived from larvae that fed on *P. padus* (Pp) or *P. serotina* (Ps) growing in high light (HL) or low light (LL) conditions. These data were expressed in relation to the total number of moths (n) that eclosed from pupae, which was set at 100%. A repeated measures ANOVA was used to assess the effect of light conditions (L), plant species (S), time (T) and their interactions on the percentage of moths that eclosed. *P* values <0.05 are in bold.

percentage of moths that eclosed. The percentage of adults that eclosed from pupae were transformed using the Bliss arc sin formula prior to conducting statistical analyses (Snedecor & Cochran, 1976). A Tukey's HSD test was employed to assess the significance of differences between all four variants. All calculations were performed using JMP software (SAS Institute Inc., Cary, NC, USA).

Results

The moths eclosed from all the cocoon bunch, in the case of shoots of *P. padus* from HL conditions and on all shoots of *P. padus* and *P. serotina* from LL conditions ($n = 10$ per variant). In the case of *P. serotina* from HL conditions, moths hatched from only 9/10 shoots. The fig. 1 shows the total number of eclosed moths for each variant (a species of *Prunus* and light conditions). The period of time over which adults continued to eclose from pupae (starting from the first moth until the last moth) was longer and less dynamic on shrubs from LL conditions than on shrubs from HL conditions (fig. 1), and was not significantly affected by the host plant. The average percentage of adult eclosion on both *Prunus* species was significantly higher (53.3%) for larvae that grazed on leaves of shrubs from LL than those that grazed on leaves of shrubs from HL conditions (44.3 vs. 68.2%; fig. 2). The host plant species had no significant effect on this parameter and there was no significant interaction also species of *Prunus* × light conditions.

A significant effect of *Prunus* species and light conditions was observed on the adult body mass of *Y. evonymellus* (fig. 3; table 1). The body mass of moths, average of both light conditions variants and both sexes, was 17.0% higher for larvae that grazed on *P. padus* as compared with those that grazed on *P. serotina*. Whereas, in the case of the effect of light, the mass of adult moths, average of both *Prunus* species and both sexes, that emerged from larvae feeding on shrubs growing in HL was 27.4% greater than those that emerged from larvae on leaves of shrubs in LL conditions. Females were 40.3% heavier than males based on the average for all variants, species and light conditions. Additionally, the mass of females

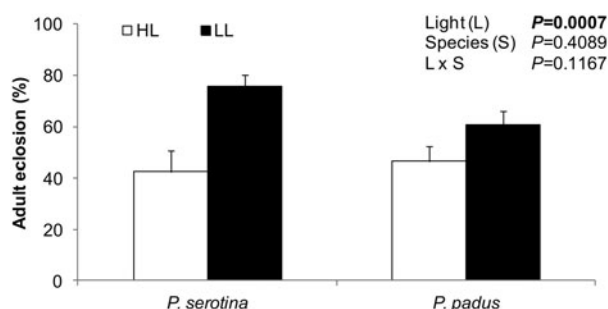


Fig. 2. Percentage of adults that eclosed from pupae derived from larvae that fed on *P. padus* or *P. serotina* growing in high light (HL) or low light (LL) conditions. These data were expressed in relation to the total number of moths that emerged from pupae, which was set at 100%. A two-way ANOVA was used to determine the significance of the observed differences in the percentages of adults that eclosed from pupae in the different conditions. Vertical bars represent SE. *P* values <0.05 are in bold.

was more strongly affected by the *Prunus* species and light conditions than the mass of males. The interaction between *Prunus* species and light conditions was also significant (table 1). Moth mass was the highest on *P. padus* growing in HL (a), followed by *P. serotina* growing in HL (b), then *P. padus* growing in LL (c), and the lowest on LL shrubs of *P. serotina* (d; Tukey's HSD test; $P < 0.05$).

The average potential fecundity was 16.3% higher for females that grazed on shrubs in HL than those that grazed on the leaves of shrubs growing in LL conditions, based on the average of both species (fig. 4). A significant effect of *Prunus* species on the fecundity of *Y. evonymellus* was also observed. An average of 31.5% more eggs were produced by females whose larvae had fed on *P. padus* shrubs as compared with those feeding on *P. serotina*.

Light conditions and *Prunus* species also had a significant effect on all of the measured wing parameters (table 2).

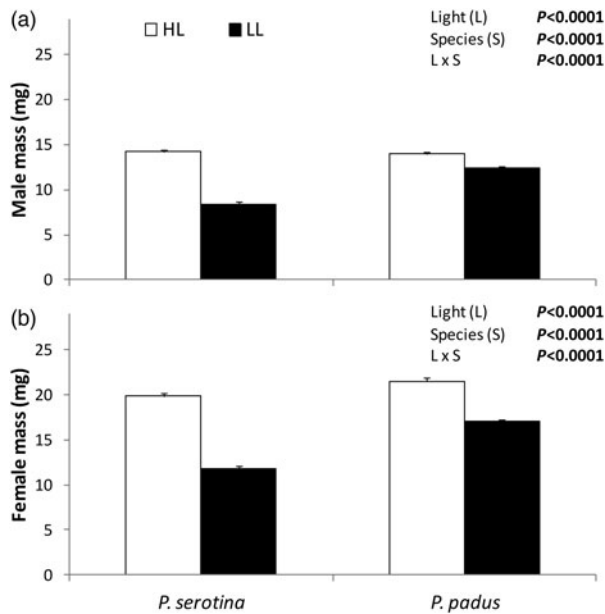


Fig. 3. Mass of male (A) and female (B) moths hatched from larvae that fed on *P. padus* or *P. serotina* shrubs growing in high light (HL) or low light (LL) conditions. A two-way ANOVA was used to determine the significance of the observed differences in the mass of both sexes from the different conditions. Vertical bars represent SE. *P* values <0.05 are in bold.

Table 1. Summary of ANOVA results (*F* and *P* values) for body mass of moths derived from larvae of *Yponomeuta evonymellus* that fed on leaves of *Prunus padus* or *P. serotina* growing in high light (HL) or low light (LL) conditions. *P* values <0.05 are in bold.

ANOVA	df	<i>F</i>	<i>P</i>
Species	1	213.09	<0.0001
Light	1	737.69	<0.0001
Species × light	1	114.23	<0.0001
Sex	1	829.30	<0.0001
Species × sex	1	17.80	<0.0001
Light × sex	1	51.17	<0.0001
Species × light × sex	1	0.80	0.3724
df error		845	

Significantly higher values were observed for nearly all of the measured wing parameters in adults whose larvae fed on *P. padus* vs. *P. serotina* and in HL vs. LL conditions. Different results were obtained only for certain parameters for the male moths that larvae fed on leaves of shrubs in HL conditions. Moreover, the interaction between *Prunus* species and light conditions was also significant for all of the wing parameters. According to Tukey's HSD test, wing parameters did not differ significantly between the host species in moths grown under HL conditions. However, in LL conditions moth had a significantly larger wings when larvae were feeding on the leaves of *P. padus* than on *P. serotina*. These relationships corresponded well with adult body mass (fig. 3). Moths, which have a higher mass have a greater wings. Female wings were always larger than male wings (table 2).

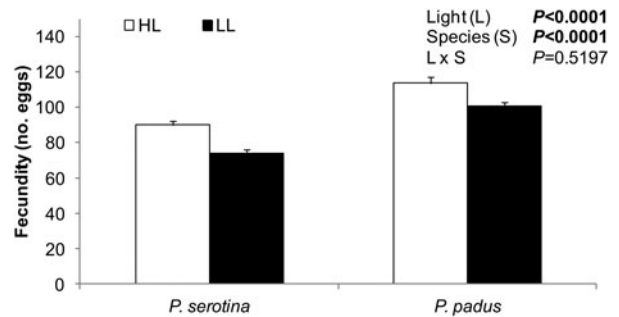


Fig. 4. Fecundity of females, as measured by the number of eggs that were derived from larvae that fed on *P. padus* or *P. serotina* shrubs growing in high light (HL) or low light (LL) conditions. A two-way ANOVA was used to determine the significance of the observed differences in fecundity from the different conditions. Vertical bars represent SE. *P* values <0.05 are in bold.

Discussion

A significant effect of *Prunus* species and light conditions was observed on the growth and development of *Y. evonymellus*. Larvae of *Y. evonymellus*, a species which is widely thought to be monophagous feeding only on native *P. padus*, can successfully survive and develop in both HL and LL conditions on the non-native shrub *P. serotina*. Among the examined variants, light conditions (HL vs. LL) had a greater effect than host species (*P. padus* vs. *P. serotina*) on the obtained results of the growth and development of *Y. evonymellus*.

The results of the present field research indicate that the light conditions under which the *Prunus* species grow significantly affect moth mass, fecundity, and all of the measured wings parameters. A higher insect mass found by us is also the most frequently used indicator of improved living and feeding conditions (Morrison & Lindell, 2012). Better host quality leads to a higher efficiency of conversion of ingested food in larvae, and thus results in increased mass in adults (Giertych et al., 2005; Niesenbaum & Kluger, 2006; Tremmel & Muller, 2013). Although some researchers indicate that leaves of shrubs growing in HL are a worse food source (higher concentration of repellents) for herbivorous insects than leaves of shrubs growing in LL conditions (Koricheva et al., 1998a; Hemming & Lindroth, 1999; Galway et al., 2004), there are also contrary evidence that are supported by our results. For example, Leather & Mackenzie (1994) found that *Y. evonymellus* that developed from larvae feeding on *P. padus* shrubs located at the edge of a forest (HL conditions) were heavier than larvae from shrubs growing deeper in the forest (LL conditions). In some cases, LL conditions can impede the growth and development of insects (Oishi et al., 2006; Muth et al., 2008; Stoepler & Lill, 2013).

Larvae of *Y. evonymellus* live gregariously until pupation (Leather, 1986). Gregariousness provides some advantages to the eggs and larvae of insects (Grégoire, 1988). Larvae jointly spin a specific silk tent in order to hide from natural enemies and raise ambient temperatures by creating a closed environment (Joos et al., 1988). Even a small increase in temperature can have a positive effect on the rate of development, final body mass or the duration of the time period in which adult insects hatch (Knapp & Casey, 1986; Łukowski et al., 2014). Considering the above, it is suggested that the performance of *Y. evonymellus* could be enhanced by the warmer

Table 2. Total wing area, forewing and hindwing area, forewing and hindwing length, and forewing and hindwing width of moths derived from larvae of *Yponomeuta evonymellus* that fed on leaves of *Prunus padus* or *P. serotina* growing in high light (HL) or low light (LL) conditions; and a summary of the ANOVA results (F and P values). Significantly higher values were observed for nearly all of the measured wing parameters in adults whose larvae fed on *P. padus* vs. *P. serotina* and in HL vs. LL conditions. Data represent the mean and SE (in parentheses). Means with the same letter are not significantly different (Tukey's HSD test; $P < 0.05$). P values < 0.05 are in bold.

Species	Light	Number of individuals		Total wing area (mm ²)		Forewing area (mm ²)		Hindwing area (mm ²)		Forewing length (mm)		Forewing width (mm)		Hindwing length (mm)		Hindwing width (mm)	
		Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
<i>P. padus</i>	HL	93	132	109.2a (1.6)	91.2c (0.9)	56.3a (0.9)	47.5b (0.5)	53.0a (0.9)	43.7c (0.5)	10.8a (0.1)	10.1b (0.1)	2.9a (0.03)	2.8b (0.02)	9.1a (0.1)	8.4b (0.1)	3.1ab (0.03)	3.0bc (0.03)
	LL	160	182	95.8b (1.0)	83.8d (0.7)	49.4b (0.5)	43.7c (0.3)	46.4b (0.6)	40.1d (0.4)	9.9b (0.1)	9.4c (0.1)	2.7b (0.02)	2.6c (0.02)	8.3b (0.1)	7.8c (0.04)	2.8d (0.03)	2.7e (0.02)
<i>P. serotina</i>	HL	60	84	104.3a (2.1)	92.3bc (1.2)	53.6a (1.0)	48.2b (0.6)	55.6a (1.1)	44.2bc (0.6)	10.7a (0.1)	10.0b (0.1)	2.9a (0.03)	2.8b (0.03)	8.9a (0.1)	8.4b (0.1)	3.2a (0.1)	3.0cd (0.03)
	LL	67	75	78.6d (1.8)	69.6e (1.5)	40.7d (0.8)	36.3e (0.7)	37.9d (1.0)	33.4e (0.8)	9.0d (0.1)	8.6e (0.1)	2.5c (0.03)	2.4d (0.03)	7.6c (0.1)	7.2d (0.1)	2.6ef (0.04)	2.4f (0.03)
ANOVA		df															
Species		1		92.47	<0.0001	95.87	<0.0001	74.10	<0.0001	85.12	<0.0001	30.74	<0.0001	76.01	<0.0001	27.23	<0.0001
Light		1		357.32	<0.0001	369.39	<0.0001	287.18	<0.0001	511.36	<0.0001	309.88	<0.0001	506.44	<0.0001	333.70	<0.0001
Species × light		1		56.38	<0.0001	59.36	<0.0001	44.44	<0.0001	49.39	<0.0001	23.58	<0.0001	33.53	<0.0001	38.82	<0.0001
Sex		1		194.15	<0.0001	175.70	<0.0001	177.89	<0.0001	135.83	<0.0001	58.46	<0.0001	126.71	<0.0001	27.23	<0.0001
Species × sex		1		6.09	0.0139	6.20	0.0130	4.97	0.0261	1.48	0.2247	0.27	0.6025	1.79	0.1816	0.84	0.3599
Light × sex		1		5.95	0.0149	4.92	0.0269	5.91	0.0153	6.84	0.0091	1.03	0.3096	4.07	0.0440	0.80	0.3719
Species × light × sex		1		0.72	0.3958	1.23	0.2681	0.29	0.5927	0.01	0.9547	0.68	0.4093	0.33	0.5651	0.87	0.3503
df error				686		686		686		686		686		686		686	

temperatures associated with high sun exposure of shrubs growing in HL conditions.

It is known fact that leaves of plants growing in HL have a higher nutritional value (content of carbohydrates and nitrogen) for folivores (Fortin & Mauffette, 2002; Oishi *et al.*, 2006; Osier & Jennings, 2007). Higher leaf nutritive values usually result in the shortened developmental duration (Tremmel & Muller, 2013), a higher body mass (Giertych *et al.*, 2005), and higher egg production (Awmack & Leather, 2002). Also in the presented research, the period over which adults continued to eclose from pupae was significantly shorter and more dynamic in larvae residing in HL shrubs than shrubs growing in LL conditions (fig. 1). In addition, body mass (fig. 3) and fecundity (fig. 4), as well as the sizes of wings (table 2), were also higher in HL shrubs as compared with shrubs growing in LL conditions. *Yponomeuta evonymellus* has been reported to exhibit a strong correlation between the size of adult females and fecundity (Kooi *et al.*, 1989; Leather & Mackenzie, 1994). Our results are in accordance to these observations.

The results presented study and our previous research (Mąderek *et al.*, 2015) indicate that the leaves of shrubs growing in HL conditions represented a higher leaf quality as food source for insects ('luxury consumption'; Muth *et al.*, 2008). As a result, the insects did not need to consume as much of this food source; consequently resulting in lower defoliation (Muth *et al.*, 2008; Karolewski *et al.*, 2013). The preference of insects for leaves of shrubs growing in HL is usually due to the presence of specific feeding stimulants such as sugars (Harborne, 1993; Levesque *et al.*, 2002). However, in the larval feeding period (April to June), the content of total nonstructural carbohydrates available to feeding larvae should be similar in both sunlit and shaded leaves (Karolewski *et al.*, 2013). As concluded in our previous paper (Karolewski *et al.*, 2014), *P. padus* and *P. serotina* leaves that were grown under the same, moderate light conditions are both comparatively high-quality foods for *Y. evonymellus* considering their chemical composition. However, under HL conditions levels of defensive compounds, such as phenolics and condensed tannins, was higher than in shrubs growing in the LL conditions, in the leaves of both the invasive *P. serotina* and native *P. padus*. Collectively, the results of the present and previous studies are consistent with the idea that monophagous insects tolerate higher levels of defense compounds in leaves than polyphagous insects (Mathur *et al.*, 2011; Ali & Agrawal, 2012; Łukowski *et al.*, 2015).

HL conditions also lead to differences in leaf structure, including greater toughness and trichome density (Molina-Montenegro *et al.*, 2006; Lukowski *et al.*, 2014; Mąderek *et al.*, 2015). In relative comparison with LL conditions, leaves of *P. serotina* in HL are characterized by greater thickness and toughness, and thus are often considered highly resistant to insect damage (Abrams *et al.*, 1992). Laboratory experiments conducted by Kooi (1989) demonstrated that *Y. evonymellus* could feed on *Prunus laurocerasus* L., a species with extremely hard and leathery leaves. Therefore, it is reasonable to consider that the increased toughness of leaves in *P. serotina* in HL conditions does not exert a negative impact on leaf consumption by *Y. evonymellus*.

Wing parameters are correlated with body mass and both strongly depend on leaf quality as food for insects (Thomas *et al.*, 1980). Similar to research of Kooi (1989), our study indicated that new host plant species has a negative effect on body mass (fig. 3) and wing size (table 2), while full light has positive effect on these parameters. Morphological plasticity of

wings as it is affected by host quality and environment parameters, may be important for the movement and survival of an insect population (Taylor & Merriam, 1995). This relationship, however, most likely depends on the insect species. In the case of *Y. evonymellus*, leaves of the native shrub *P. padus* growing in HL conditions appear to be a more optimum food source.

A benefit derived from feeding on HL leaves is that it shortens the time period over which adults continue to eclose from pupae. This in turn, further reduces the time that an insect is exposed to natural enemies during a vulnerable stage (fig. 1) which may be important to the reproductive success of *Y. evonymellus*. The quality of the host plant used by males and females during larval instars may significantly affect the reproductive success of both sexes (Delisle & Hardy, 1997).

Light conditions affected the percentage of pupation, which was higher for larvae that grazed on leaves of LL shrubs rather than leaves of shrubs growing in HL (fig. 2). These results may be due to the variable occurrence and activity of natural enemies. Predatory and parasitic organisms have been widely investigated and evaluated as biological control agents (Unruh *et al.*, 2003; Barber & Marquis, 2011). Natural enemies, such as other insects (Stoepler & Lill, 2013) and arthropod predators (Skoczylas *et al.*, 2007; Barber & Marquis, 2011) are often more abundant on fully sunlight (HL) than on shaded (LL) plants.

The *Y. evonymellus* moth reaches sexual maturity a few days after leaving the pupa but further dissemination of adults is a small distance (Menken *et al.*, 1992; Javoš *et al.*, 2005). In this scope, the size of the wings may therefore be important. Furthermore, the simultaneous eclosion of many individuals that are capable of reproduction creates a potential opportunity to achieve a high level of reproductive success (Bakker *et al.*, 2011). Moreover, higher fecundity is also a crucial factor that increases the transmission of the gene pool. Summarizing, better performance of insects mentioned above seem to confirm the higher quality of *Prunus* shrubs growing in HL than LL conditions for *Y. evonymellus* that was also previously postulated (Leather & Mackenzie, 1994; Łukowski *et al.*, 2014).

The present study provides a more comprehensive understanding of the phenomenon of the adaptation of *Y. evonymellus* to a new host plant and different light conditions within the host plant. This is especially relevant in the context of changing climate – global warming and drought; namely the displacement of *P. padus* by the invasive *P. serotina*. From an ecosystem perspective, it is interesting that the effect of light conditions (HL vs. LL) on the performance of this folivorous insect varied between the two host species. Such differential effects on host plant – insect interactions could potentially alter the successional dynamics of moth communities. The long-term displacement of *P. padus* by the invasive *P. serotina* could result in a gradual adaptation by *Y. evonymellus* to use the leaves of shrubs growing in HL conditions. Better growth and development of moths that larvae feeding on *P. serotina* shrubs growing in HL conditions implies that this insect may be observed to be more willing to use shrubs located in open, sunlit forest areas in the future. Since insects play a major role in the transfer of energy from plants to higher trophic levels, it is important to determine the effect of alien plants on size of the insect population and their biomass (Tallamy, 2004). The effect of neophytes on insect body mass may have far-reaching consequences on ecosystem structure and the complexity of ecological interactions (Heleno *et al.*, 2009). It is too early to predict, however, the extent to which *Y. evonymellus* will adapt to using *P. serotina* leaves and

whether this broadening the base of hosts plant will impact the spread of this invasive shrub in European forests. Further studies pertaining to the adaptation of *Y. evonymellus* to a new host plant are required to determine the factors determining oviposition and population parasitism in *Y. evonymellus*.

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