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ORIGINAL ARTICLE

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Effects of defoliation by horse chestnut leafminer (*Cameraria ohridella*) on reproduction in *Aesculus hippocastanum*

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Abstract In large parts of Europe horse chestnut trees (*Aesculus hippocastanum*) suffer from severe defoliation by an alien invasive species, the specialist leaf mining moth *Cameraria ohridella* (Lepidoptera; Gracillariidae). Heavily infested trees have a drastically shortened period for photosynthesis. We quantified the effect of moth infestation on reproduction of horse chestnut trees in two different cities in central Europe, Bern and Munich. *C. ohridella* negatively affected seed and fruit weight of *A. hippocastanum* at both locations. In Munich, seed weight of heavily damaged trees was reduced by almost half. However, the number of seeds per fruit, the number of fruits per inflorescence, and the number of inflorescences per tree did not change due to herbivory. We conclude that *C. ohridella* mining affects seed quality but not seed quantity. The reduced seed weight may severely impair growth and survival of horse chestnut seedlings and thus may endanger the long-term persistence of *A. hippocastanum* in its endemic forests in south-east Europe.

Keywords Herbivory · Seed size · Tree · Fruit abortion · Imidacloprid

Introduction

Since 1984, a new pest of unknown origin – the horse chestnut leafminer (*Cameraria ohridella* Deschka and Dimic, Lepidoptera, Gracillariidae) – has spread out dramatically from Macedonia via Austria over the rest of Europe. This invasive moth species attacks almost exclusively the white flowering horse chestnut (*Aesculus hippocastanum* L., Hippocastanaceae). Larvae of the moth feed on the leaf parenchyma between the two epidermis layers thereby reducing the amount of photosynthetically active tissue. In summer defoliated horse chestnut trees are already common. However, the anticipated dieback of adult *A. hippocastanum* trees (Butin and Führer 1994; Kenis and Forster 1998) has so far not been observed. More subtle effects of leafmining may concern the reproduction of the tree. Rearing of ornamental horse chestnut trees takes place in tree nurseries and is considered to be not at risk, because chemical insect control can be effectively applied to seedlings and young plants. Thus, in urban settings damage caused by *C. ohridella* is restricted to premature loss of leaf area in adult trees, thereby preventing them from properly contributing to a balanced urban microclimate, and to aesthetical problems with defoliated trees. By contrast, in the native region of horse chestnut in south-east Europe, where *C. ohridella* also occurs at high densities (Trenchev et al. 2000; Avtzis 2003), tree recruitment in the endemic forests occurs naturally either by seeds or vegetatively by sprouts growing out of the roots of established trees, and therefore may be affected by leafmining.

Herbivory often affects plant reproduction (Obeso 1993; Crawley 1997). There are either direct effects of herbivory (reduction of the amount of photosynthetic active tissue thereby impairing the production of assimilates) or indirect effects, e.g. induction or maintenance of defense mechanisms, which may be associated with costs for the plants (Bergelson and Purrington 1996; Purrington 2000; Strauss et al. 2002). The response of plants to herbivory is variable, whereby herbs show a larger range of compensatory responses to herbivory than woody plants (Paige and Whitham 1987; Obeso 1993; Haukioja and Koricheva 2000; but see Bergelson and Crawley 1992). In general, woody plants exhibit a negative growth response to herbivory, and there are – to our knowledge – no compelling reports of enhanced reproduction after herbivore attack (but see Sacchi and Connor 1999). However, most of the studies only measured the initial response to herbivory after the first season and compen-

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sation may occur after a time lag (Crawley 1985; Obeso 1993; Kaitaniemi et al. 1999; Cobb et al. 2002).

Reproduction of *A. hippocastanum* in response to herbivore damage by *C. ohridella* can be affected quantitatively, for example by a reduction in the number of seeds produced per tree. When the actual resource level is lowered by herbivory, fewer seeds per fruit may be developed (Stephenson 1980) or selective fruit abortion may alter the number of matured fruits per inflorescence (Stephenson 1980; Niesenbaum 1996). Also the total number of inflorescences produced per tree may be altered. Reproduction may also be affected qualitatively, for example by a reduction in the weight of individual seeds (Kaitaniemi et al. 1999). The number of seeds produced and seed size or weight are important factors for successful seedling establishment (Crawley 1983; Stanton 1984; Hutchings 1997; Turnbull et al. 2000). As a consequence the long-term natural succession in the Balkan forests may be altered by the moth, and may even lead to the replacement of *A. hippocastanum* in the last remaining endemic refuges of the species.

In this paper we investigate the impact of *C. ohridella* on reproduction of *A. hippocastanum.* The aim of our study was to quantify the effect of leaf mining on both the quality (seed and fruit weight) and quantity of horse chestnut seeds (number of seeds per fruit, number of fruits per inflorescence, number of inflorescences per tree).

Materials and methods

Study species

The horse chestnut is a monoecious, broad-leaved deciduous tree. Its native region is southeastern Europe (Bulgaria, Macedonia and Greece) where at present the only natural stands are glacial relicts (Ulbrich 1928; van der Pijl 1982) of the species located in canyon forests. In urban areas throughout Europe, *A. hippocastanum* is a very popular ornamental tree in public parks, alleys and as sunshade in private areas such as gardens or restaurants. The flowers of *A. hippocastanum* are aggregated in inflorescences. During fruit maturation up to eight echinated fruits develop per inflorescence (personal observation). Fruits contain six seeds, but only a subset of them grows to viable seeds able to germinate.

Larvae of the horse chestnut leafminer *C. ohridella* feed on the parenchyma between the two epidermal layers inside horse chestnut leaves. Depending on climatic conditions the moth develops between two and four generations per year. In each generation a fraction of the pupae does not hatch immediately but stays in the leaves and enters diapause (Freise and Heitland 2001). The moths hibernate in the pupal stage in the litter and a new moth generation hatches in spring.

Experimental set-up and procedure

In Munich, ripe fruits were collected from the trees at 62 sites on 9 September 1998. The sites were classified into three infestation categories according to the damage caused by *C. ohridella* (leaf area lost, LAL): 22 sites were assigned to the low infestation category (<25% LAL), 27 to the medium infestation category (25%–75% LAL) and 13 to the high infestation category (>75% LAL). LAL was estimated visually at the time of the most intense seed fall (in September). To ensure an accurate estimation of LAL, a sequence of reference pictures with various levels of moth infestation where LAL was measured digitally by image analysis (IMAQ Vision Builder, National Instruments) was made in advance and used in the field.

After the collection, seeds were dried for 4 days at 110°C, cooled down in an desiccator and immediately weighed to determine their dry weight (DW). Only seeds >1 g fresh weight (FW) were included in the study, because previous experiments showed that smaller seeds do not germinate (Thalmann and Bacher, unpublished data). Mean seed weight, mean fruit weight (total weight of all seeds contained in a fruit) and the mean number of seeds (>1 g) per fruit were determined per site.

In Bern, from 15 trees with low infestation rates (<1% LAL) and another 15 trees with medium to high moth infestation rates (>10% LAL) about 30 fruits each were arbitrarily collected from the lower tree parts (up to a height of 6 m) on 24 September 2001 at the beginning of fruit fall. LAL was determined as described above. All trees selected were of similar size and were not pruned. Fruit and seed FW was determined immediately after harvest.

For the assessment of the number of fruits produced per inflorescence 18 trees with low moth infestation levels (<25% LAL) and 10 trees with high infestation levels (>25% LAL) were investigated in 2000. Trees were pre-selected because of their infestation level in 1999. Only trees that fitted the assigned infestation level in autumn 2000 were considered further. All trees selected were of similar size and were not pruned. Of each tree, 15–20 inflorescences were marked in spring and re-visited in late summer (10 August 2000) to record the number of fruits produced per inflorescence.

The effect of leaf mining on the number of inflorescences produced per tree was investigated in Bern in a moth exclusion experiment. At one site, 30 alley horse chestnut trees standing in a row were divided into ten blocks of three successive trees each. All trees were of similar size, were not pruned and experienced the same degree of moth infestation in 2000. After flowering, one randomly chosen tree of each block was treated with stem injections of the systemically active insecticide Confidor (Bayer; active substance imidacloprid), one with water injections and one served as control. On 2 October 2001 the LAL due to *C. ohridella* mining was estimated. Before the first insecticide application (14 May 2001) the 30 trees were photographed. On 6 May 2002 the trees were photographed again from the same positions as the year before. To account for differences between individual trees in the number of inflorescences produced we calculated the ratio of inflorescences produced in the years after and before moth exclusion. Because it was not feasible to count all inflorescences of the trees on the photographs we compared the number of inflorescences produced on parts of the trees that were clearly visible on the photographs in 2002 with the number of inflorescences produced on the same parts in 2001.

Statistical analysis

Comparisons of means were made by analysis of variance (ANOVA) with either three (Munich) or two moth infestation groups (Bern). For detection of differences in means between the three groups (results from Munich) Scheffé's post-hoc test was performed. Data on the ratio of inflorescences per tree 2002/2001 were ln+1 transformed. For this experiment a model I two-factorial ANOVA was performed (block: random factor; treatment: fixed factor). To compare the number of inflorescences per tree observed in 2001 with those observed in 2002 we used the Wilcoxon test. In the moth exclusion experiment, percentage values of the infestation levels were arc sin square root transformed. Data were compared with a model I two-factorial ANOVA (block: random factor; treatment: fixed factor). For detection of differences in means between the three treatments (insecticide, water, control) a Tukey HSD post-hoc test was performed. All analyses were performed with the software package SPSS version 10.

Results

The intensity of herbivore attack of *C. ohridella* had a significant effect on seed and fruit weight of *A. hippocastanum*, both in Munich (Fig. 1a, Table 1) and in Bern (Fig. 1b, Table 1). Trees with high moth infestation level showed a significantly reduced seed and fruit weight compared to less infested trees. In Munich seed and fruit weight of trees in the high infestation class (>75% damage) were significantly reduced compared to trees in the medium and low infestation classes. The number of seeds developed per fruit was not significantly affected by *C. ohridella*, neither in Munich (Fig. 2a, Table 1) nor in Bern (Fig. 2b, Table 1). No significant effect of *C. ohridella* infestation on the number of fruits per inflorescence (Fig. 3, Table 1) and the ratio between the number of inflorescences of a tree part in the year 2002 and 2001 (Fig. 4, Table 1) was detected. The insecticide-treated trees had a LAL of 22%.

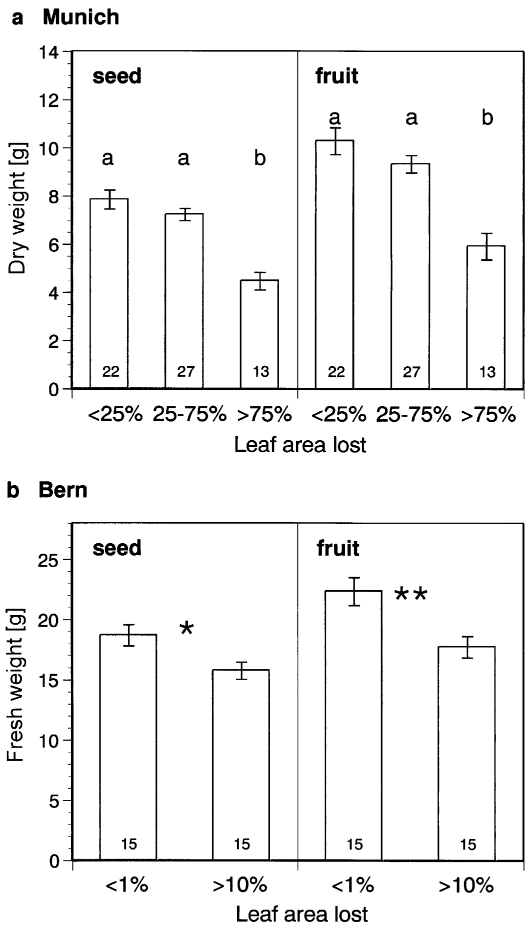

Fig. 1 Effect of different infestation levels of *Cameraria ohridella* on seed weight and fruit weight (mean±SE) of *Aesculus hippocastanum* in **a** Munich (1998) and **b** Bern (2001). In **a** bars that share a common letter are not significantly different from each other at *P*<0.05; Scheffé's post-hoc test after one-way ANOVA. In **b** bars with one asterisk (*) are significantly different at the *P*<0.05 level; two asterisks (**) at the *P*<0.01 level. Numbers at the bottom of the bars represent sample size

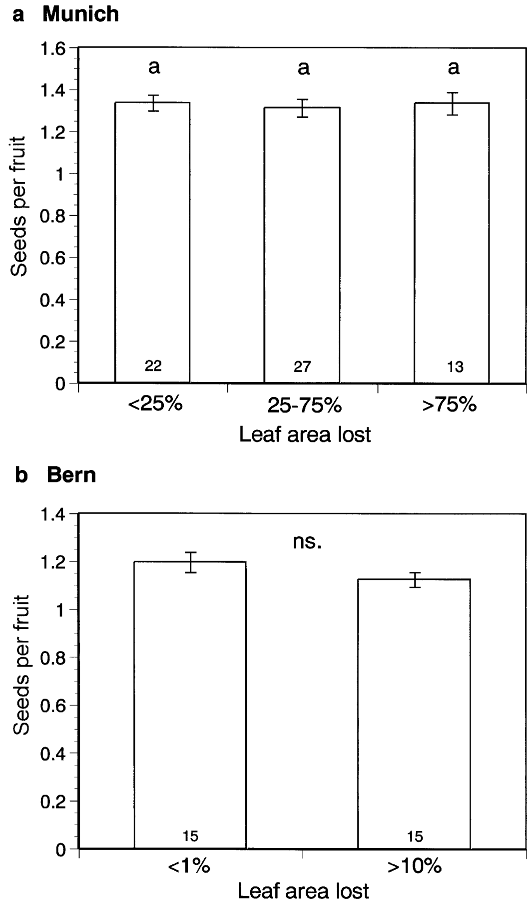

Fig. 2 Effect of different infestation levels of *C. ohridella* on number of seeds developed per fruit (mean±SE) of *A. hippocastanum* in **a** Munich (1998) and **b** Bern (2001). In **a** bars that share a common letter are not significantly different from each other at *P*<0.05; Scheffé's post-hoc test after one-way ANOVA. In **b** ns. means not significant. Numbers at the bottom of the bars represent sample size

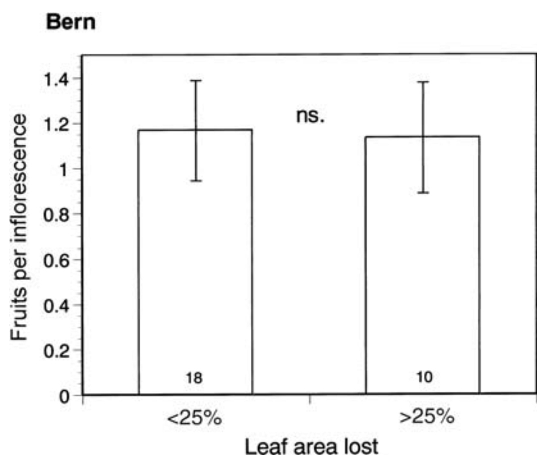

Fig. 3 Effect of different infestation levels of *C. ohridella* on number of developed fruits per inflorescence (mean±SE) of *A. hippocastanum* in Bern (2000). ns. Not significant. Numbers at the bottom of the bars represent sample size

Table 1 ANOVA table of the effects of *Cameraria ohridella* on different reproduction parameters of *Aesculus hippocastanum* in Munich in 1998 and in Bern in 2000 and 2001. Sample size in Munich was 62. Sample size in Bern was 28 and 30 trees. The parameters analyzed were: (1) seed weight (Munich dry weight, Bern fresh weight), (2) fruit weight (Munich dry weight, Bern fresh weight), (3) number of seeds per fruit, (4) number of fruits per inflorescence, and (5) ratio between observed inflorescences in 2002 and 2001

Location, year of study	Source	*df*	MS	*F*	Significance
(1) Seed weight					
Munich 1998	Infestation category	2	49.73	21.59	<0.001
	Residuals	59	2.30		
	Total	61			
Bern 2001	Infestation category	1	64.62	6.72	0.015
	Residuals	28	9.62		
	Total	29			
(2) Fruit weight					
Munich 1998	Infestation category	2	81.28	16.88	<0.001
	Residuals	59	4.81		
	Total	61			
Bern 2001	Infestation category	1	159.16	9.81	0.004
	Residuals	28	16.22		
	Total	29			
(3) Number of seeds per fruit					
Munich 1998	Infestation category	2	0.003	0.09	0.91
	Residuals	59	0.04		
	Total	61			
Bern 2000	Infestation category	1	0.04	1.84	0.185
	Residuals	28	0.02		
	Total	29			
(4) Number of fruits per inflorescence					
Bern 2000	Infestation category	1	0.01	0.01	0.925
	Residuals	26	0.79		
	Total	27			
(5) Ratio inflorescences 2002/2001					
Bern 2001	Block (random factor)	9	0.20	1.81	0.14
	Treatment (insecticide, water, control) (fixed factor)	2	0.07	0.61	0.56
	Residuals	18	0.11		
	Total	29			

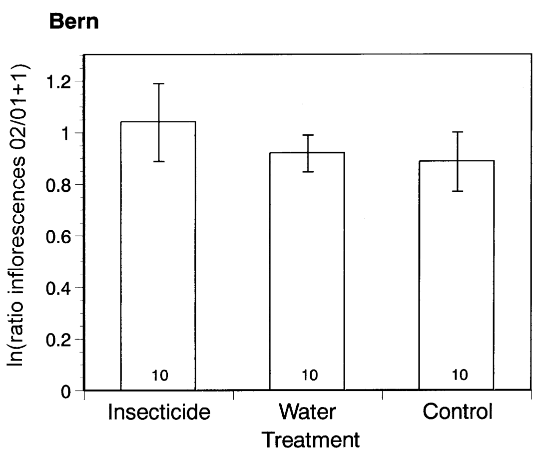

Fig. 4 Effect of different infestation levels of *C. ohridella* on the ratio of inflorescences of 2002 and 2001 (mean±SE) in Bern. Three treatments were applied to totally 30 trees: Insecticide injections, water injections, and controls. Numbers at the bottom of the bars represent sample size

The control trees and the water-treated trees showed an average LAL of 48% respectively of 49%, which was not significantly different (Tukey HSD: P=0.99). Insecticide-treated trees had a significantly lower LAL compared to the two other groups (Tukey HSD: P<0.001). The total number of inflorescences was higher in the second year of the experiment (number of inflorescences 2001: 74.5±55, mean±SD; 2002: 106.2±70.7; Wilcoxon-test P=0.001).

Discussion

Larval mining of *C. ohridella* caused severe damage in heavily infested *A. hippocastanum* at both experimental locations. In Munich infestation is documented since 1994 (Heitland et al. 2000), in Bern since 1997 (S. Bacher, personal observation). The time period in which highly infested *A. hippocastanum* can assimilate photosynthetic products is drastically shortened compared to uninfested trees or other tree species. Some of the stressed trees even flowered for a second time in autumn (personal observation).

Our results demonstrate that the damage caused by *C. ohridella* negatively affects seed and fruit weight of *A. hippocastanum*. In Munich seed weight of heavily damaged trees was reduced by almost half compared to less damaged trees. A reduction in seed weight was observed for measurements of both seed dry weight (Munich) and fresh weight (Bern). This indicates a putative different water content of the seeds of the different infestation categories was not responsible for the weight alteration. The reduction of seed weight of highly infested trees is also consistent with the findings of Salleo et al. (2002); they also found a substantial reduction of seed dry weight due to *C. ohridella* infestation in north-eastern Italy. There is a general pattern in plants that large seeds perform better than small seeds; they usually grow higher, survive better, and are better competitors (e.g. Stanton 1984; Armstrong and Westoby 1993; Leishman and Westoby 1994; Hutchings 1997; Seiwa 2000). The consequence of reduced seed weight may be finally an alteration of plant succession (Davidson 1993; Carson and Root 1999). From our own studies on *A. hippocastanum* we know that seedlings from large seeds grow taller and survive better under interspecific competition than seedlings from small seeds (Thalmann and Bacher, unpublished data).

On the other hand, we did not find indications that the number of seeds produced per tree is affected by moth infestation. Leaf removal due to herbivory reduces the resources available to trees for growth and reproduction. Regardless of resource availability *A. hippocastanum* did not reduce the number of seeds produced per capsule. *C. ohridella* mining also did not affect the number of fruits produced per inflorescence, i.e. the level of available resources did not affect the number of aborted fruits. This is in contrast to other studies demonstrating that herbivory significantly affects the extent of seed abortion in woody plants (Stephenson 1980; Lee 1988; Niesenbaum 1996). Selective abortion of fruits and selective allocation of resources to the remaining fruits containing embryos of higher genetic quality is regarded as a possible reaction of the tree to varying resource availabilities (Janzen 1977; Stephenson 1981). Also at the tree level no significant alteration in the number of inflorescences produced was observed after 1 year of moth density reduction. Protected trees did not use the additionally available assimilates to produce more inflorescences.

In summary, *A. hippocastanum* trees respond to defoliation by *C. ohridella* with a reduction in seed quality, but not in seed quantity. However, some tree species may react with a time lag to altered resource availability. For example, Kaitaniemi et al. (1999) showed in mountain birch that the bud type determination and subsequently the number of catkins were affected by defoliation that occurred 2 years before. Long-term studies are necessary to detect such time lags.

Trees as iteroparous long-lived species can be expected to behave as typical K-strategists (Pianka 1970). *A. hippocastanum* trees should therefore react to current bad conditions, such as strong herbivore pressure, by first ensuring their own survival and growth at the cost of reducing the current allocation of resources to reproduction (Crawley 1997; Haukioja and Koricheva 2000). Results in this paper and the findings of Salleo et al. (2002) support this hypothesis. Salleo and co-workers even found a 62% increase in wood production of *A. hippocastanum* since the arrival of *C. ohridella* with a 28% increase in conductive xylem area, which would permit an almost threefold higher theoretical sap flow. This increase in hydraulic efficiency may improve the provisioning of the remaining intact leaf tissue and so partly compensates for the damage (Crawley 1997) caused by *C. ohridella*. However, although the survival and growth of individual horse chestnut trees does not seem to be impaired by *C. ohridella* defoliation, the reduced seed weight may severely impair growth and survival of horse chestnut seedlings and thus may endanger the persistence of *A. hippocastanum* in the endemic forests in south-east Europe.

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