Herbivore Impact Versus Host Size Preference: Endophagous Insects on *Heracleum mantegazzianum* in Its Native Range

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ABSTRACT   Classical biological control is a practice to control alien invasive weeds, but many introduced biological control agents exhibit only a weak negative impact on their targets. One reason is that prerelease impact studies in the natural environment are often difficult to carry out. *Heracleum mantegazzianum* Sommier and Levier (Apiaceae), which is native to the Caucasus, is a perennial noxious weed introduced into Europe and North America. We examined the impact and host size preference of different endophagous insect guilds in the weed's native range. Instead of the commonly used insect exclosure approach, we estimated plant vigor before and after herbivore attack under natural conditions. Endophagous herbivores were dominated by the weevil species *Lixus iridis* Olivier, *Nastus fausti* Reitter, and *Otiorhynchus tatarchani* Reitter (Coleoptera: Curculionidae), the fly *Melanagromyza heracleana* Zlobin (Diptera: Agromyzidae), and an unidentified root-boring agromyzid fly species. Most observed insect species exhibited a strong preference for either big or small plants, but none of them caused serious damage within the study period. Occurrence of root-feeding weevils was associated with weak plants, but because of their long larval development, it was not possible to assign this relationship clearly to either feeding damage or host size preference. A comparison with other studies indicated that mature *H. mantegazzianum* plants are quite tolerant to herbivory. Insects belonging to the feeding guilds studied here will probably not guarantee successful biological control. Further research should focus on earlier stages in the weed's life cycle.

KEY WORDS   *Heracleum mantegazzianum*, classical biological control, invasive weed, prerelease impact assessment, host size preference

Classical biological control of weeds, the introduction of exotic natural enemies, is an increasingly prevalent practice of controlling alien invasive plant species (Julien and Griffiths 1998, McEvoy and Coombs 1999). Besides host specificity, a main demand on biological control agents is that they have a negative impact on its host's vigor. However, many introduced biological control agents have only weak effects on their target weeds after release (Williamson and Fitter 1996, Julien and Griffiths 1998, Louda et al. 2003), which can even lead to a negative impact on the competing native plant species they were intended to support (Callaway et al. 1999, Pearson and Callaway 2003). In the debate on the risk to native species associated with biological control (Louda et al. 2003), less attention has been paid to the efficiency of introduced biological control agents. A significant contribution to minimizing environmental risk would be achieved through eliminating the release of ineffective agents (McEvoy and Coombs 1999). However, the urgently needed further development of protocols for prerelease impact evaluation is still under discussion (Louda et al. 2003).

Prerelease impact assessment of phytophagous insect species in the weed's native range is difficult to carry out (Wapshere 1985). Many herbivorous insects do not randomly choose their hosts even among conspecific plants for feeding and ovipositioning, but are selective in several ecological factors such as nutrient quality, spatial or temporal plant distribution, plant structure, competition, or predation (Price et al. 1980, Karban 1989, Ballabeni et al. 2001, Fujiyama et al. 2003). Some herbivores have a host size preference (Briese et al. 2003, Smith and Story 2003) and herbivory usually causes sublethal damage, a problem with impact studies is to distinguish between host selectivity and herbivore impact. If, for example, attacked plants show a decreased performance compared with noninfested plants, the herbivore could either be damaging the host or preferring small or weak plants. However, a negative impact can be masked by a preference for vigorous plants. Even though female oviposition preference is usually positively correlated with plant size (Price 1991, Inbar et al. 2001), there are also examples where smaller plants are more likely to be attacked (Forsberg 1987).

To counteract this problem, the majority of impact studies use exclosure experiments with field cages or

insecticides to compare the performance of plants exposed to herbivores with those protected from them (Maron and Vila 2001). An essential assumption in exclosure experiments using insecticides is that the treatment has no direct effect on plant growth. However, many studies have shown diverse physiological and ecological changes including phytotoxic or plant growth promoting effects, increased nutritive value, changes in attractiveness for herbivores or parasitoids, direct and indirect effects on predators and parasitoids, and the activation of detoxification pathways in herbivores for a broad range of insecticides (Hardin et al. 1995, Straw et al. 1996, Haile et al. 2000). Manipulation of insect densities with field cages is a common method, but it becomes more complicated with increasing plant size. In addition, cages may protect potential biological control agents against natural enemies. Therefore, the efficiency of biological control candidates could be overestimated, because predation and parasitism were repeatedly reported to inhibit the establishment of biological control agents in their new environment (Goeden and Louda 1976). We chose a different approach in this study, adapted to characteristics of giant hogweed, *Heracleum mantegazzianum* Sommier and Levier (Apiaceae).

Giant hogweed is a monocarpic perennial plant (Tiley et al. 1996), which can reach a height of up to 4 m. The plant is native to the alpine and subalpine belt of the Western Caucasus, from where it was introduced to Europe as an ornamental plant in the early 19th century (Ochsmann 1996). Since its introduction, giant hogweed has been spreading with increasing rapidity (Pysek 1991), and thus has become an important weed in central and northern Europe, Canada, and northern parts of the United States (Tiley et al. 1996). The ability of the seeds to float often results in a distribution along watercourses, but it also invades various other habitats, particularly disturbed areas and meadows (Pysek 1994). Like other members of the family, *H. mantegazzianum* contains phototoxic furanocoumarins with insecticidal properties (Berenbaum 1978). The plant sap, in combination with UV radiation, causes blisters and burns on contact with human skin (Lagey et al. 1995).

In this study, we tried to distinguish between host size preference and herbivore impact by measuring the variables associated with plant vigor before and after herbivore infestation. The impact of phytophagous larvae on plant fitness was estimated by their abundance relative to the calculated plant growth rate. To assess the host size preference, we studied the correlation between insect occurrence and plant vigor. The main focus was on endophagous insects, which seem to be more often host specific than ectophages (Cornell and Kahn 1989, Gaston et al. 1992). Until now, no such experiments have been conducted in the native area of giant hogweed. Hence, this study gives a first estimation on the impact of Caucasian insect species and insect guilds on *H. mantegazzianum.*

Materials and Methods

Study Areas and Sampling. During the 2002 growing season, five field surveys to 14 different *H. mantegazzianum* populations were conducted in the Russian Caucasus (approximately monthly from mid-May until early October). Many of the locations were visited several times. The altitude ranged from ≈500 to 2,000 m above sea level.

Based on our experience in the previous season, we organized two field surveys in 2003 to the Russian Caucasus (20–27 June and 18–31 July). According to Otte and Franke (1998), the initial seed production of *H. mantegazzianum* takes place only 6 wk after the beginning of the regenerative development. Our observational time covered a large part of this period. On each trip, we visited the same two *H. mantegazzianum* populations, one located in the Arhyz nature preserve (43°39′18″ N, 41°24′59″ E, 1,710 m a.s.l.) and the other on a long-abandoned field near the village Pregradnaja (43°54′27″ N, 41°17′02″ E, 920 m a.s.l.). Each population was comprised of several hundred adult individuals. Different altitudes and the resultant difference in climatic conditions, especially the shift in the beginning of the vegetation period, is the primary distinction between the two localities. In the following, we will refer to these as the upper and lower locations.

During our first trip, we established two transects at each location. Along each transect, we tagged 24 plants in the rosette stage and measured the length of each leaf. Flower shoots had just begun to grow, so stem-feeders apparently did not attack before this measurement. At the second visit, we additionally measured fresh weight of all plant organs (root, leaves, terminal flowering shoot, satellite flowering shoots, terminal inflorescence, and satellite inflorescences, with a Pesola spring scale, 2,500 g). All roots and stems were dissected and the number of larvae was recorded. In accordance with Otte and Franke (1998), we assumed that all plants that flowered during the observation were in their third year, and all nonflowering plants in rosette stage were in their second year.

Insects. The most common endophagous insects on giant hogweed belong to the orders Coleoptera and Diptera. We frequently found three weevil species (Coleoptera: Curculionidae): *Nastus fausti* Reitter, *Otiorhynchus tatarchani* Reitter (found only at the upper location at Arhyz), and *Lixus iridis* Olivier (found only at the lower location). The larvae of *N. fausti* and *O. tatarchani* are root feeders and are not distinguishable in the larval stage under field conditions. We detected them inside the root and at the root's surface. Larvae of *L. iridis* develop inside the hollow stems. Flies were mainly represented by a stem boring agromyzid, newly described as *Melanagromyza heracleana* Zlobin (2005) (Diptera: Agromyzidae), and an unidentified root-boring agromyzid species.

Lixus iridis and *O. tatarchani* develop on different plant genera in the Apiaceae. Therefore, their use related to biological control of *H. mantegazzianum* is limited. Results belonging to this species can only be

Table 1. Proportion of *H. mantegazzianum* plants attacked by different endophagous insects (numbers in parenthesis represent average no. of larvae per attacked plant)

Percent attacked plants	Stem feeder (3-yr-old plants)			Root feeder (3-yr-old plants)			Root feeder (2-yr-old plants)		
	n	L. iridis[a]	M. heracleana	n	N. fausti O. tatarchani[b]	Agromyzidae	n	N. fausti O. tatarchani[b]	Agromyzidae
Lower location	30	83 (4.7)	60 (22)	30	30 (2.6)	77 (7.0)	17	6 (3.0)	0
Upper location	20	0	90 (44)	20	20 (1.3)	60 (4.2)	27	11 (1.5)	0

[a] Occurred only at the lower location.
[b] Occurred only at the upper location.

used for the identification of plant parts, which are sensitive to herbivory. The host range limits of the other herbivores are not exactly known. Further comments on the dietary requirements are given in the discussion.

Preference and Impact Assessment. To estimate the plant biomass at the beginning of our observational time (henceforth referred to as the initial plant biomass), we measured the size and weight of 111 leaves not included in the experiment during our first survey. Curve estimation provided a suitable equation to determine leaf weight $\{\ln(\text{weight}) = \ln(0.07) + [2.07 \times \ln(\text{length})]; r^2 = 0.89\}$. Stem weight, as far as present, at the first survey was calculated as the stem weight at the second survey multiplied by the ratio of the stem lengths of both visits. To evaluate host size preference of the insect species, we analyzed the relationship between larval abundance and log-transformed initial plant biomass using linear regression.

After log-transformation of the variables regression analysis showed that the initial plant biomass exhibited a clear linear relationship with the final plant biomass measured on the second survey (log-biomass$_{\text{final}}$ = $-0.01 + 1.06 \times$ log-biomass$_{\text{initial}}$; $r = 0.90$) as well as with the umbel weight (log-weight$_{\text{umbel}}$ = $-0.10 + 0.8363 \times$ log-biomass$_{\text{initial}}$; $r = 0.73$). If an insect species has a negative impact on the plant, high larval densities should be associated with plants whose observed final biomass and umbel weights are lower than the values predicted by the regression model. Therefore, we studied the relationship between the occurrence of insect larvae and the residuals from the regression to assess the herbivore impact.

The central premise of our host size preference and impact assessment is that oviposition roughly coincided with our first survey and that feeding damage of developing larvae occurred mainly between both visits. This is certainly the fact for the stem-boring insects, because flower stems just started to develop during the first survey. Spot tests during the first visit and the developmental stage of the root-boring agromyzid fly larvae indicates that this assumption is most likely true for this species. On the contrary, the life cycle of the root-boring weevils is comparatively long. Oviposition and larval feeding started in the previous season. For this reason, it was not possible to split the relationship between plant and insect performance in selectivity and impact. Therefore, both possibilities will be discussed.

Linear regressions were conducted for each plant variable and each insect species separately. Only the mature 3-yr-old plants were included in the analyses, because insect performance on plants in rosette stage was too low to calculate a meaningful regression. Plant variables were log-transformed to normalize the residuals. Location was included in the models as a binary predictor when the related insect species occurred on both plant populations. All statistical analyses were performed with SPSS 12.

Table 2. Regressions analyses of herbivore insect species and plant variables of mature *H. mantegazzianum*

Regression model	Initial biomass				Final biomass				Umbel wt			
	β	t	P	r^2	β	t	P	r^2	β	t	P	r^2
Stem feeder												
Lixus iridis	−0.40	−2.29	0.03	0.16	−0.10	−0.55	0.58	0.01	−0.11	−0.58	0.57	0.01
M. heracleana	0.59	4.61	<0.001	0.43	−0.00	−0.01	0.99	0.19	0.20	1.59	0.12	0.38
Location	0.10	1.53	0.13		0.43	2.96	0.005		−0.67	−5.32	<0.001	
Root feeder												
N. fausti, O. tatarchani	−0.33	−2.56	0.01	0.29	−0.09	−0.66	0.52	0.19	−0.14	−1.15	0.25	0.35
Location	0.38	2.97	0.005		0.42	3.10	0.003		−0.60	−4.94	<0.001	
Agromyzidae gen. spec.	0.27	2.08	0.04	0.25	−0.16	−1.18	0.24	0.21	0.18	1.42	0.15	0.36
Location	0.46	3.56	0.001		0.41	3.14	0.003		−0.56	−4.68	<0.001	

A significant relationship between no. of insect larvae and initial plant biomass indicates host size preference for small (negative standardized β weights and t-values) or big plants (positive β and t). Herbivore impact was estimated with associations between larval abundance and final plant biomass or the wt of all umbels (both adjusted for initial plant biomass). Plant variables are log-transformed. Except for *L. iridis,* the location was included in the models as binary predictor (0 = lower location, 1 = upper location).

Results

Insect Abundance. The occurrence of endophagous herbivores associated with giant hogweed is summarized in Table 1. We found stem-boring *L. iridis* larvae inside almost each hogweed plant at the lower location but never at the upper location. In addition, we never found adults or larvae in altitudes above 1,300 m during the 2002 surveys. Therefore, *L. iridis* might be absent in high altitudes. Larvae of *M. heracleana* were very common in both plant populations and reached a maximum density of 135 larvae per plant. The infestation rate was significantly higher at the upper location ($\chi^2 = 5.36$; $P = 0.02$). The number of insects per plant was also increased. Root-feeding weevil larvae were the least common species but repeatedly found at both locations on 3-yr-old plants; occasionally, they also occurred on 2-yr-old plants. Root-feeding Diptera attacked mature plants at significantly higher frequency in the lower location. They were never found on 2-yr-old plants. Because root-boring fly larvae are sometimes located in deep secondary roots, the real number might be somewhat higher.

Selectivity and Impact of Stem-boring Insects. Both insect species showed a significant host size preference. High quantities of *L. iridis* larvae were associated with small *H. mantegazzianum* plants. Their number decreased significantly with increasing initial plant biomass (Table 2; Fig. 1b). The *M. heracleana* larvae showed an opposite pattern. High numbers were prevalent found inside bigger plants (Table 2; Fig. 1a). Both insect species exhibited no negative impact on *H. mantegazzianum.* Neither the final plant biomass nor the weight of umbels as indicators for changes in plant development after herbivore attack showed a reaction to either larval density of *L. iridis* or to *Melanagromyza* larvae (Table 2; Fig. 2a and c).

Selectivity and Impact of Root-Boring Insects. Abundance of root-boring Agromyzidae was positively correlated with the initial plant biomass (Table 2; Fig. 1c), indicating a preference for larger plants by ovipositing female flies. The final plant biomass and the weight of umbels are not affected, so impact on plant development is absent (Table 2; Fig. 2b and d). In case of the weevil species *N. fausti* and *O. tatarchani,*

the regression coefficient is negative in the initial plant biomass analysis (Table 2; Fig. 1d). The final plant biomass and the umbel weight showed no response to the presence of larvae (Table 2; Fig. 2b and d). The coefficients of the regression analysis indicate in addition that regional distinctions explain a significant proportion of the variation of the plant variables (Table 2). The decreased final plant biomass at the lower location is based on the fact that the ground leaves, which constitute a considerable part of total plant biomass, start senescing with the beginning of the generative development (Otte and Franke 1998). Because of the earlier start of the vegetation period at the lower location, the reproductive growth and simultaneous decomposition of ground leaves is more advanced compared with the upper location. In contrast to the final biomass, the umbel weight was in average higher at the lower location.

Discussion

Most observed insect species showed a distinct host size preference for either small or big plants, whereas the observed impact on plant vigor appeared negligible. Most plants at the lower location started fruiting during our second survey. From there it is unlikely that the herbivores are able to cause serious damage later in the year. In contrast to the other observed insect species, the larval development of the root-feeding weevils takes almost 1 yr and started long before the beginning of our study. It is difficult to state whether the relationship between feeding traces and reduced plant vigor is associated with herbivore damage or with oviposition preference for weak plants. The observed reduction of plant biomass and flower weight could be a meaningful contribution to reduce plant competition. According to the plant-vigor hypothesis (Price 1991), many herbivores prefer to feed on vigorous plants, because they are more nutritious. Therefore, preference for weak plants should be an exception. However, there are also several reasons why small plants could be more suitable for herbivores (Mayhew 1997). For instance, stress conditions, like limited resources, could lead to reduced plant growth
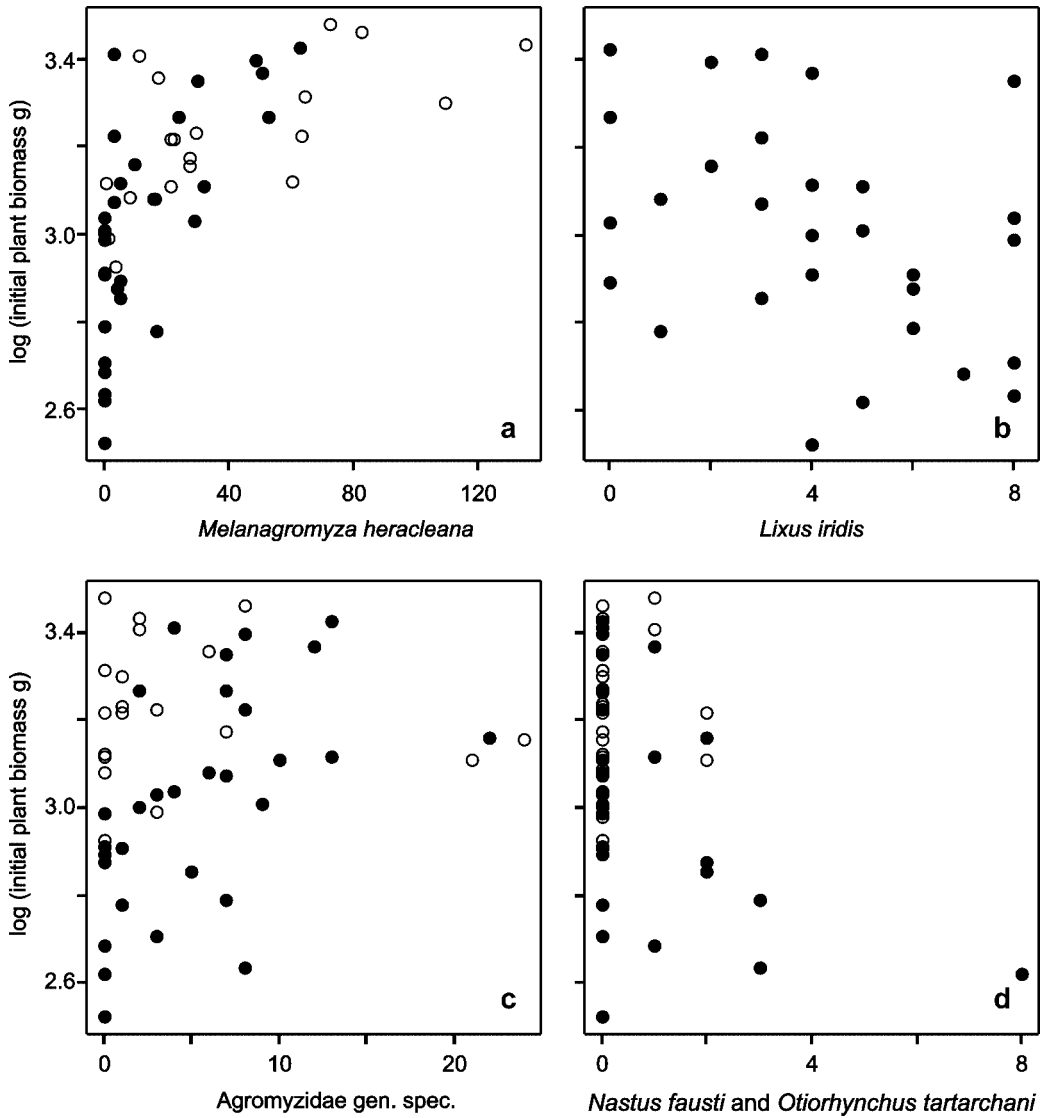
Fig. 1. Relationship between occurrence of herbivore larvae and initial plant biomass of mature *H. mantegazzianum* as measure for host size preference. ○, upper location; ●, lower location.

and to decreased allocation of defensive compounds at the same time (White 1984). Studies investigating these two contradictory hypotheses have yielded inconsistent results (Inbar et al. 2001), indicating that the interactions are more complex and other important factors are involved.

It is possible that root-feeding weevil larvae living externally in the beginning of their live cycle are boring into the roots after a certain time. This could explain why we only occasionally found damaged roots of biennial plants. The larval development of almost 1 yr should result in similar infestation rates of biennial plants after oviposition and triennial plants before pupation, if we disregard plant and insect mortality. Nevertheless, it is difficult to generalize about our results derived only from one field season because

herbivore impact is known to depend on several factors (e.g., weather conditions) and can differ from year to year (Dhileepan 2003, Russell and Louda 2004).

It is possible that only the interaction of several antagonists will lead to a meaningful impact. According to McEvoy and Coombs (1999), there currently exists no general conclusion whether successful biological control is usually related to one effective control agent as assumed by Myers (1985) or to the interaction of small effects caused by several antagonists (Schroeder and Goeden 1986). Although some studies associated with biological control showed a mutualistic relationship of the effectiveness of different antagonists (Bacher and Friedli 2002), the interactions of several weed antagonists do not necessarily result in a
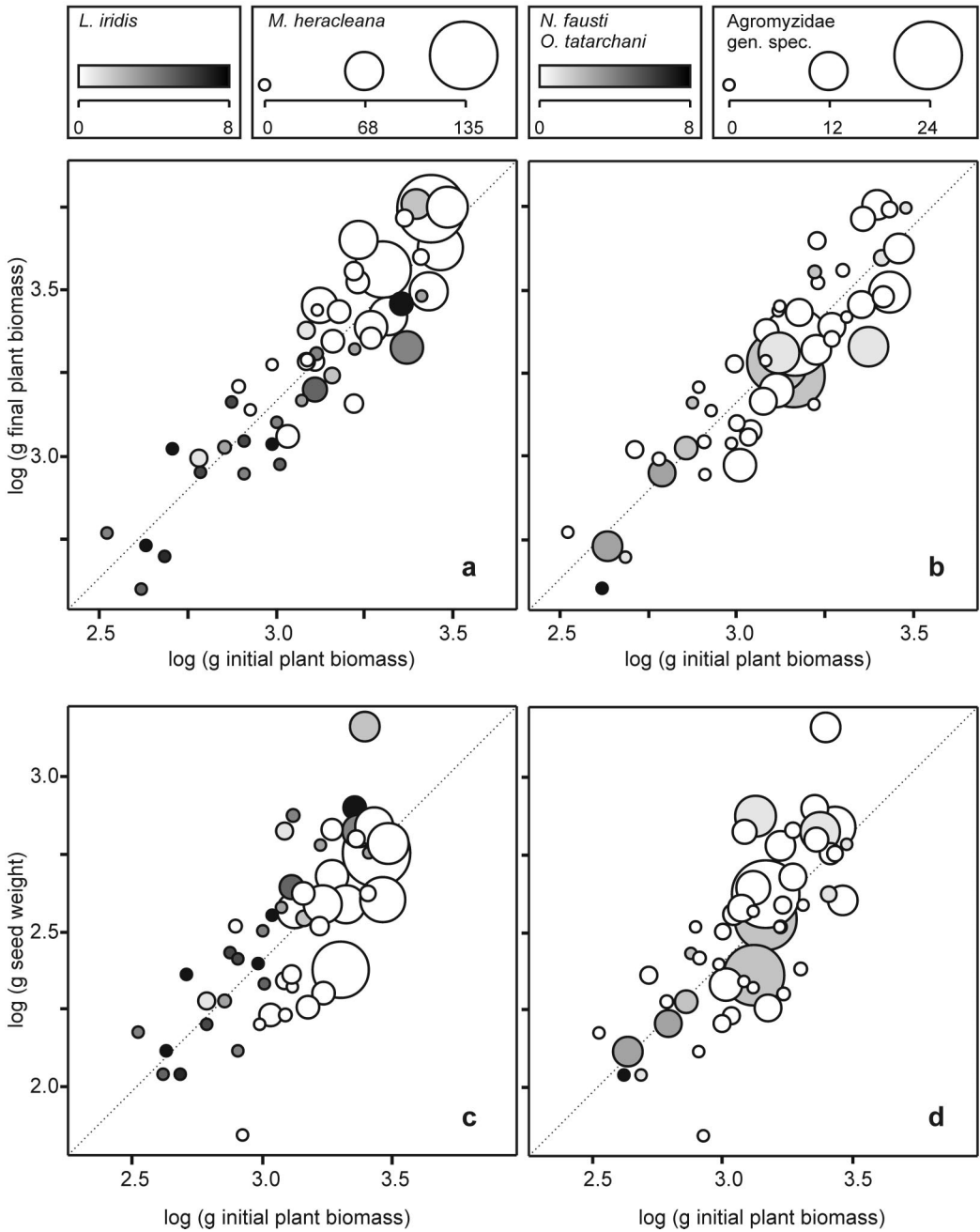
Fig. 2. Impact of stem feeding (a and c) and root boring (b and d) insects on biomass (a and b) and seed production (c and d) of mature *H. mantegazzianum*. Plant variables are adjusted for the initial plant biomass. The dotted line is the mean prediction line calculated from linear regression. Symbols below the prediction line represent plants with lower biomass or seed production than expected from their initial biomass. Dark or large sized symbols represent plants attacked by many Curculionidae or Agromyzidae larvae, respectively.

cumulative effect; they can even affect each other negatively. For example, adults of the leaf beetle *Cassida rubiginosa* Muell. avoid thistles, *Cirsium arvense* L., infected with the fungus *Phoma destructiva* Plowr. for oviposition and feeding. Both were formerly con-

sidered as potential biological control agents (Krüss 2002).

Some studies have reported serious damage on *Levisticum officinale* Koch (Eichler 1951) and *Heracleum sosnowski* Manden. (Volovnik 1988) caused by *L. iri-*

dis. Unfortunately, both quantified neither the level of attack nor the reduced plant fitness. However, it seems that tolerance to herbivory is pronounced in mature *H. mantegazzianum* compared with other plants. The preference of *L. iridis* to smaller plants results from the morphology of the proboscis. Females bore cavities into their host stems for oviposition. As a consequence, the stem wall has to be thinner than the length of the rostrum of the beetle. Eber et al. (1999) found that body size of *Lixus elongatus* Goeze is positively correlated with the host stem diameter. This means that they exhibit a host size preference for larger plants within their morphological restrictions. Thus, the large size of giant hogweed is probably responsible for the fact that we found most larvae in the smallest size class. In addition, we found all larvae of *L. iridis* in the upper narrow parts of the flower stem. On the contrary, thick stems provide a greater food source for *M. heracleana*, which oviposit in the outer layer of the stem. The larvae were mostly located in the lower part of the stem. This opposite preference leads to a specialization in separate niches in plant individuals, perhaps to avoid interspecific competition (Zwölfer and Brandl 1989). Detailed within-plant distribution is discussed elsewhere (Hattendorf 2005).

The host range of potential agents is a critical factor in biological control. *Lixus iridis* and *O. tatarchani* are known to feed on several plant genera; therefore, they are not suitable as biological control agents. The reproduction of *O. tatarchani* was parthenogenetic in the laboratory. Because exotic biological control agents have to adapt to exploit the new habitat and target weed, a high level of genetic diversity would be preferable. However, Roderick and Navajas (2003) found no evidence that genetic adaptation is important for the success of insect biological control agents. The diet of *N. fausti* is not known in detail yet. According to Arzanov et al. (1996), adults are widespread in the forest belt of the Caucasus and were repeatedly found on leaves of *Heracleum. M. heracleana* and the undetermined root-boring agromyzid fly are in terms of dietary requirements more promising. Many members of this family seem to be highly host-specific; 79 of 87 agromyzids on Apiaceae are at least restricted to this plant family (Spencer 1990). However, because of the big size of giant hogweed, it could be difficult to develop mass-rearing techniques for the stem-feeding *M. heracleana.* Another species of the genus *Melanagromyza, M. eupatoriella* (Spencer), was suggested as a biological control agent for the weed *Chromolaena odorata* L. R. M. King and H. Rob., but several attempts failed to rear it in quarantine (Lorraine and Zachariades 2002).

In conclusion, most phytophagous insects showed a strong host size preference for either big or small plants. Because this behavior seems to be widespread, at least in herbivores on giant hogweed, the development of future protocols for prerelease impact studies should take account of this situation. For plant species with a more suitable size, the manipulation of herbivore densities with field cages should be additionally be carried out. Even if side effects like predation remains unclear, a potential bias caused by host size preference can be excluded. However, the approach used here could be suitable if the situation in the weed's native range is largely unknown, as in our case, or if population dynamics of the potential biological control agent are likely to be strongly top-down regulated. The negative impact of the examined insect species on the weed was small. This study suggests that mature giant hogweed plants can tolerate rather high herbivore loads. Further studies should try to identify more crucial stages in the weed's life cycle.

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