

# Evaluation of *Nastus fausti* Reitter (Coleoptera: Curculionidae: Entiminae: Nastini) for Biological Control of Invasive Giant Hogweeds (*Heracleum* spp.)

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**Abstract**—The weevil *Nastus fausti* Reitter (Coleoptera, Curculionidae) was evaluated for its potential in the biological control of invasive giant hogweeds (*Heracleum* spp.). Quantitative sampling suggested that at a high population density (more than 3–4 mature larvae per plant) damage by *N. fausti* larvae could have some negative impact on the above-ground part of the plant. However, no-choice laboratory tests showed that *N. fausti* females were able to feed on a number of Apiaceae genera, including such important cultivated crops as carrot, parsnip, and celeriac. Feeding on these plants did not cause any significant decrease in female survival or fecundity. Moreover, at least part of *N. fausti* larvae may feed and develop on roots of these plants, and the rate of their growth and development does not differ significantly from that in larvae fed on roots of *H. mantegazzianum*. *N. fausti* adult and larval feeding on *Angelica purpurascens*, representative of related genus of the same tribe, was recorded under natural conditions, too. In combination, these data suggest that *N. fausti* is an oligophagous species connected with plants from at least several genera of Apiaceae and thus it cannot be considered a potential agent for biological control of invasive *Heracleum* species.

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## INTRODUCTION

The so-called “giant hogweeds” are a group of closely related Apiaceae species (*Heracleum mantegazzianum* Sommier et Levier, *H. sosnowskyi* Manden, and *H. persicum* Desf. ex Fischer), naturally growing in the Caucasus, Transcaucasia, and the Near East (Jahodová et al., 2007). Recently, giant hogweeds invaded Europe posing a serious threat to natural biodiversity and human health (Thiele and Otte, 2007). Various methods were proposed to control giant hogweeds (Nielsen et al. 2007; Ravn et al., 2007). However, biological control is the most effective and environmentally friendly way to cope with biological invasions (McFadyen, 1998; Goeden and Andres, 1999). Field explorations conducted in the Western Caucasus, within the natural range of *H. mantegazzianum*, revealed a number of phytophagous insects feeding on this plant (Hansen et al., 2006, 2007; Cock and Seier, 2007). Particularly, root boring larvae and leaf chewing adults of *Nastus fausti* Reitter were repeatedly collected. As this weevil was not yet recorded in the area invaded by giant hogweeds in Western Europe, it

was considered as a potential biocontrol agent. However, data on its host specificity and impact on the host plant are still poor and contradictory, being based on occasional observations rather than on special field or laboratory studies (Arzanov and Davidyan, 1995; Hansen et al., 2006, 2007; Cock and Seier, 2007).

The present study was mostly aimed at testing the host specificity of *N. fausti* larvae and adults in the laboratory and under natural conditions. In addition, its abundance and impact on the host plant in native habitats were also estimated.

## MATERIAL AND METHODS

Under natural conditions, *N. fausti* adults were manually collected from leaves of *H. mantegazzianum* and other plants. One- and two-year old (not yet flowering) giant hogweed plants were sampled. Usually, the totals of inspected plants and of collected insects were calculated for a population. For a special quantitative sampling, the number of living (green) leaves, the length of a longest leaf, the base of the root dia-

**Table 1.** *Nastus fausti* distribution and abundance by the results of field collections conducted in 2005

Serial number of the inspected population, its geographic and ecological description <sup>1</sup>	Date of collection, number of inspected plants (pl.), collected <i>N. fausti</i> larvae (larv.), pupae (pup.), and adults (ad.) <sup>2</sup>		
	23–30.IV	2–10.VIII	26.IX–1.X
1. Karabeshgonka River, env. of Zelenchukskaya, Karachay–Cherkess Rep. 43°53'02"N, 41°32'15"E, 907 m. Old field. Black soil.	pl. = 50 larv. = 2		
2. Env. of Leso-Kefar, Karachay–Cherkess Rep. 43°48'51"N, 41°28'07"E, 1028 m. Old field, meadow. Black soil.	pl. = 160 larv. = 4	pl. = 80	
3. Env. of Arkhyz, Karachay–Cherkess Rep. 43°39'17"N, 41°24'59"E, 1745 m. Meadow, forest margin. Mountain meadow stony soil.	pl. = 25 larv. = 24	pl. = 76 larv. = 8 pup. = 6	pl. = 56 larv. = 41 ad. = 1
4. Env. of Arkhyz, Karachay–Cherkess Rep. 43°39'22"N, 41°23'31"E, 1330–1400 m. Forest clearing. Mountain forest soil.	pl. = 15 larv. = 3		
5. Teplaya river, env. of Kobu-Bashi, Karachay–Cherkess Rep. 43°54'30"N, 41°17'05"E, 920–940 m. Old field, meadow. Black soil.	pl. = 93 larv. = 17	pl. = 223 larv. = 30	pl. = 188 larv. = 40 pup. = 1 ad. = 2
6. Shapka hill base, env. of Pregradnaya, Karachay–Cherkess Rep. 43°56'39"N, 41°06'14"E, 924 m. Old field, meadow. Black soil.		pl. = 83 larv. = 17	pl. = 50 larv. = 177 pup. = 6 ad. = 3
7. Env. of Psebay, Krasnodar Terr. 44°09'55"N, 40°51'35"E, 560–600 m. Meadow. Black soil.	pl. = 55		
8. Env. of Tulsy, Krasnodar Terr. 44°30'37"N, 40°09'08"E, 280 m. River bank, wet meadow. Black soil.	pl. = 25 larv. = 1 ad. = 2		
9a. Env. of Gubskaya, Krasnodar Terr. 44°20'13"N, 40°40'31"E, 419 m. Boggy meadow. Swampy soil.		pl. = 20	
9b. Env. of Gubskaya, Krasnodar Terr. 44°20'06"N, 40°40'31"E, 427 m. Forest windbreak, meadow. Black soil.		pl. = 30 larv. = 19	pl. = 51 larv. = 161 pup. = 16 ad. = 6
10. Env. of Guseripl, Krasnodar Terr. 44°00'59"N, 40°03'29"E, 1070–1230 m. Roadside, forest margin. Mountain forest grey stony soil.	pl. = 40		
11. Env. of Samurskaya, Krasnodar Terr. 44°17'13"N, 39°50'10"E, 260 m. Forest clearing. Mountain forest grey soil.		pl. = 50 larv. = 15	pl. = 31 larv. = 27 pup. = 5 ad. = 5
12. Env. of Smolenskaya, Krasnodar Terr. 44°44'07"N, 38°44'01"E, 33 m. Old field, forest windbreak. Black soil.		pl. = 32	

Notes: <sup>1</sup> Terr. = territory, Rep. = republic; env. = environs; <sup>2</sup> zero values for larvae, pupae, and adults are not given. Empty cells mean absence of data.

meter, the number of *N. fausti* larvae feeding on the root, and the degree of damage to the root (scores from 0 to 3) were separately recorded for each plant. To

count larvae, roots were visually examined and then longitudinally dissected. In addition, soil within a radius of 10–15 cm and 20–25 cm deep was inspected.

Usually, a total of 50–100 roots per location were studied (Table 1).

In the laboratory, host specificity was studied in three experiments. In all cases, no-choice tests were conducted, i.e. only one plant species was offered to each individual insect.

**(1) Females survival, feeding and oviposition under no-choice conditions in Petri dishes.** This experiment was conducted in a thermostatic chamber at 20°C and 18 h light day. Ovipositing females collected in their natural habitats were individually placed in Petri dishes with bunches of leaves of tested plant species. During the whole experiment, one plant species was offered to each female. Every second day, the food was replaced and the eggs laid were counted. Thus, for each female the following characteristics were recorded: total fecundity (the total number of eggs laid by a female during the period of observation), oviposition intensity (the mean number of eggs laid by a female per day), life duration (days from the beginning of the experiment), and feeding intensity (recorded every second day, simultaneously with the food replacement, as scores: 0 - no feeding, 1 - slight nibbling, 2 - small damage, 3 - normal damage typical of feeding on the native host plant).

**(2) Female oviposition and larvae development on potted plants.** In this experiment, ovipositing females were individually placed in small cages installed on pots with test plants (in each cage, only one plant was present). In 5 days, females were removed and then test plants were periodically observed for the signs of larval damage (discoloration, wilt). If such signs were detected, the root was dug out, dissected and carefully inspected for larvae and/or for traces of larval feeding. Forty days after the beginning of the experiment, all roots of the remaining plants were dissected. The result of the test was considered as positive if at least one living larvae or evident traces of larval feeding were found. In addition, the suitability of the tested plant for *N. fausti* larvae growth and development was quantitatively estimated by measuring the size (head capsule width) of larvae. Larvae collected from *H. mantegazzianum* under natural conditions were used as controls.

**(3) Growth and development of the first instar larvae transferred on plants.** In this experiment, neonate larvae hatched from eggs laid by females used in the first experiment were transferred with a fine brush onto the soil surface close to the stem base of a

potted test plant. Only the progeny of control females fed on *H. mantegazzianum* leaves was used. Then, the soil was abundantly watered, to facilitate larvae movement to the roots. Since the main aim of this test, as that of the two preceding experiments, was to check host specificity under the most provocative conditions, a mixture of progenies of different females was used and numerous larvae (up to 50–100 per plant, depending on its size) were transferred. The results of this experiment were recorded as described for the second test.

Most of the recorded parameters were extremely variable and did not correspond to the normal distribution. Thus, not only means, but also medians, quartiles, and range were used as descriptive statistics. All calculations were made with SYSTAT software.

## RESULTS AND DISCUSSION

### *Morphology, Systematic Position and Brief Review of the Bionomics*

*Nastus (Neonastus) fausti* Reitter, 1888.

—*circassicus* Reitter, 1888 : 259; Arzanov and Davidian, 1995 : 628–631.—*lederi* Reitter, 1888 : 259; Arzanov and Davidian, 1995 : 628–631.

Beetles of medium and large size, body length (without rostrum) 5.4–11.5 mm. *N. fausti* is wingless, like all its congeners. Weevils rather quickly run and easily climb plants, which is facilitated by long legs with strongly developed femoral teeth and broad tarsi with dense adhesive sole brushes. Freshly emerged adults have characteristic long mandibular appendages which are lost when the adults start feeding. The males are more slender and usually smaller than females; they possess broader femora and fore tarsi; the inner face of hind tibiae is covered with long, silky light hairs in distal half.

According to the recent review of the Caucasian *Nastus* species (Arzanov and Davidian, 1995), *N. fausti* includes two subspecies: *N. fausti fausti* and *N. fausti taya* Arzanov et Davidian. The differences between the two subspecies are not very sharp and refer to details of the structure of the rostrum and sculpture of the pronotum.

*N. fausti* is characterized by a broad variation of body size (even within a population, some individuals could be twice as large as the others) and coloration. Usually the dorsal side of the body is densely but not contiguously covered with more or less elongate

**Table 2.** Influence of *Nastus fausti* population density, *Heracleum mantegazzianum* root size and degree of its damage on the number of living leaves and on the length of the longest leaf (the results of field sampling conducted during 26.09–1.10.2005)

Population (see table 1 for detailed description)	<i>Nastus fausti</i> population density (larvae / root)			Degree of <i>H. mantegazzianum</i> root damage, scores from 0 to 3 (mean±SD)	Influence of degree of root damage on parameters of the above-ground part of the host plant (regression coefficient <i>R</i> and its significance)	
	mean ± <i>SD</i> , <i>n</i>	quartiles	range		number of living leaves	length of the longest leaf
3. Arkhyz	0.7 ± 1.4, <i>n</i> = 52	0–1	0–8	2.0 ± 1.0	<i>R</i> = – 0.07	<i>R</i> = – 4.0
5. Teplaya	0.2 ± 0.5, <i>n</i> = 148	0–0	0–3	1.4 ± 1.1	<i>R</i> = 0.05	<i>R</i> = – 0.2
6. Shapka	3.5 ± 4.8, <i>n</i> = 40	0–5	0–20	2.1 ± 1.0	<i>R</i> = – 0.35 *	<i>R</i> = 3.8
9b. Gubskaya	3.2 ± 3.8, <i>n</i> = 47	1–4	0–16	2.7 ± 0.5	<i>R</i> = – 0.32	<i>R</i> = – 3.9
11. Samurskaya	0.9 ± 1.4, <i>n</i> = 26	0–2	0–5	1.7 ± 0.9	<i>R</i> = – 0.03	<i>R</i> = – 6.7

Note: \* Significance of the regression coefficient:  $p < 0.05$ .

scales. The vestiture is one-colored, light grey or brownish, occasionally with a bronze reflection; or a pattern is formed of light speckles on a dark, occasionally almost black background; the speckles of broadly varying shape and size mostly concentrate along elytral striae.

*N. fausti* can be distinguished from its close allies by the following combination of characters: pterygia rounded; front not wider than rostral dorsum at the level of antennal insertions; pronotum with median carina; elytral striae well defined; dorsal side of aedeagus flat or slightly convex, ventral side with well developed median carina.

Development lasts for one or two years. Adults occur from the end of April to the beginning of August, being most abundant for a short period in the second half of May and in June. Most of the daytime they spend on plants, usually on the upper side of leaves, less commonly on stems and leaf stalks. These beetles feed, cutting the leaf margins, and mate. When disturbed, beetles retract their legs and drop from a plant. Females lay eggs on the soil surface near the host plant. The larvae live in the soil and feed on roots. The body of the larva is white, with long erect hairs; the head capsule is light brown. Pupation proceeds in the soil chamber near the root system of the host plant. Adults emerge mostly in the first half of autumn, most of them remain in the soil for hibernation

and leave their hibernation places only in the subsequent spring.

#### *Distribution, Abundance, and Impact on Host Plant*

*N. fausti* is one of the most widespread and abundant species of this genus. It is an endemic insect of the Caucasus spread over a wide territory from Gendzhik to Ingushetia in the North Caucasus and to the Gudauta district of Abkhazia in Transcaucasia. *N. fausti* inhabited a wide range of altitudes from foothills (200–300 m a.s.l.) to the low alpine zone (2000 m a.s.l.). This species is very common in mesophil meadows of the tall grass zone along rivers and streams, in forest clearings, and also in subalpine zone. In the forest, these beetles are much rarely found (Arzanov and Davidyan, 1995).

In 2005, field collections were conducted over a large part of the native area of *H. mantegazzianum*. Larvae of *N. fausti* were found in 10 of the 13 inspected giant hogweed populations (Table 1). Quantitative sampling revealed rather high density in some of the inspected populations (Tables 1, 2).

In September of the same year, a special quantitative sampling was conducted in 5 populations (Table 2) to estimate the impact of damage caused by larval feeding on the host plant growth. In certain cases, it was not possible to exactly count all larvae feeding on a given plant, as some larvae were found in

the soil between two neighboring plants. Moreover, the damage was dependent not only on the number of larvae, but also on their age. Besides, some larvae already terminated feeding and pupated before sampling. Thus, the degree of damage (*DD*) was visually estimated as scores from 0 to 3. As could be expected, the degree of root damage significantly, although not very closely ( $r = 0.42$ ,  $n = 376$ ,  $p < 0.001$ ) correlated with the number of larvae feeding on the plant. The aboveground part of the plant (leaf rosette) was described by two characteristics: the number of living leaves (*LN*) and the length of the longest leaf (*LL*), both parameters being strongly positively correlated with the root diameter (*RD*). Thus, the General Linear Model method was used to analyze the results. For the pooled data from all records ( $n = 313$ ), both characteristics of the plant growth negatively depended on the degree of damage to the root ( $LN = 1.1 + 0.28 RD - 0.06 DD$  and  $LL = 21.5 + 9.4 RD - 2.1 DD$ ), but both dependencies were insignificant ( $p = 0.28$  for *LN* and  $p = 0.19$  for *LL*), while the dependence on the root diameter for both parameters was very strong ( $p < 0.001$  for both regressions).

When data from each population were treated separately (Table 2), regression coefficients were negative in 8 cases of 10, although only in one case (population no. 6, Shapka hill) this dependence was significant. Note that in the same population the maximal mean population density of *N. fausti* was recorded (Table 2).

When the data from two populations with the high *N. fausti* population density (Shapka hill and Gubskaya) were pooled, the dependence of the number of leaves on the degree of damage was highly significant:  $LN = 1.5 + 0.40 RD - 0.42 DD$  ( $n = 87$ ,  $p < 0.002$  for both factors), while the length of the longest leaf still depended significantly ( $p < 0.001$ ) only on the root diameter:  $LL = 8.5 + 14.4 RD - 0.3 DD$  ( $n = 87$ ).

Thus, we conclude that under natural conditions *N. fausti* larvae could cause some negative impact on *H. mantegazzianum* plants only at rather high insect population density (more than 3-4 old instars larvae per root). Such a high threshold of damage could be explained by the large size of giant hogweeds (in studied populations, mean root diameter of 1-2 years old plants was ca 3 cm) and the high regeneration ability of the plant (Pyšek et al., 2007).

#### Host Specificity

*N. fausti* are known to be trophically connected with hogweeds (Arzanov and Davidyan, 1995) and, particu-

larly, it was repeatedly collected from *H. mantegazzianum* (Hansen et al., 2006, 2007).

Host specificity tests were conducted with adults collected under natural conditions (Table 1, populations no. 5, 6, and 9b). Plants were grown in a greenhouse, the following plant species were used for the tests:

(1) *Heracleum mantegazzianum* Sommier & Levier grown from roots collected in Gubskaya (Table 1, population no.9b).

(2) *Heracleum sosnowskyi* Manden grown from roots collected in the environs of St. Petersburg.

(3) *Heracleum sibiricum* L. grown from roots collected in the environs of St. Petersburg.

(4) *Heracleum asperum* (Hoffm.) M. Bieb. grown from roots collected in Gubskaya (Table 1, population no.9b).

(5) *Angelica purpurascens* (Ave-Lall.) Gilli grown from roots collected in Gubskaya (Table 1, population no.9b).

(6) *Angelica sylvestris* L. grown from roots collected in the environs of St. Petersburg.

(7) *Angelica litoralis* Fries grown from roots collected in the environs of St. Petersburg.

(8) *Pastinaca sativa* L. (parsnip) grown from roots purchased in agricultural shops.

(9) *Thyselium palustre* (L.) Rafin. grown from roots collected in the environs of St. Petersburg.

(10) *Chaerophyllum aureum* L. grown from roots collected in Gubskaya (Table 1, population no.9b).

(11) *Apium graveolens* L. (celeriac) grown from roots purchased in agricultural shops.

(12) *Daucus carota* L. (carrot) grown from roots purchased in agricultural shops.

**Feeding of females and oviposition in Petri dishes.** As seen from Table 3, the average life duration does not significantly depend on the species of the plant used to feed the female ( $p = 0.16$ , Kruskal-Wallis test). The influence of plant species on the feeding intensity was highly significant ( $p = 0.001$ ), although the "natural" host plant, *H. mantegazzianum* and some other tested plant species induced practically the same feeding intensity. The total lifetime fecundity during the experimental period also significantly depended on the food plant ( $p = 0.014$ ). However, paired compari-

**Table 3.** Food plant species influence on survival, feeding intensity, and oviposition of *Nastus fausti* females in Petri dishes<sup>1</sup>

Food plant species and number of females tested ( <i>n</i> )	Life duration (days)	Feeding intensity (scores 0–3)	Total fecundity (eggs / female)	Oviposition intensity (eggs / female / day)
<i>Heracleum mantegazzianum</i> ( <i>n</i> = 16)	13 (6–22) [4–40]	2.9 (2.8–3.0) [2.0–3.0]	154 (94–310) [20–630]	12.0 (9.4–16.9) [5.0–35.7]
<i>Heracleum sosnowskyi</i> ( <i>n</i> = 9)	10 (8–12) [0–20]	2.2 *** (1.8–2.5) [0.0–2.8]	87 (30–175) [0–198]	10.9 (8.2–13.4) [3.8–15.3]
<i>Heracleum sibiricum</i> ( <i>n</i> = 9)	18 (6–30) (4–32)	2.7 ** (2.0–2.8) [1.5–2.9]	258 (93–339) [9–594]	14.9 (8.8–18.4) [2.3–18.8]
<i>Heracleum asperum</i> ( <i>n</i> = 6)	14 (12–16) [6–18]	1.7 *** (1.5–1.8) [1.5–2.5]	171 (140–246) [116–251]	15.6 (8.4–20.9) [7.3–23.3]
<i>Angelica purpurascens</i> ( <i>n</i> = 5)	21 (21–28) [10–40]	2.6 (2.5–2.7) [2.5–3.0]	255 (248–338) [138–502]	12.1 (8.9–13.8) [8.4–23.9]
<i>Angelica sylvestris</i> ( <i>n</i> = 7)	17 (13–20) [7–21]	2.8 (2.5–2.9) [2.3–3.0]	239 (220–265) [167–336]	16.9 (13.2–19.8) [10.4–23.8]
<i>Angelica litoralis</i> ( <i>n</i> = 6)	5 (3–21) [0–23]	2.8 (1.0–3.0) [0.0–3.0]	84 (49–170) [0–342]	14.9 (9.8–16.8) [8.1–27.7]
<i>Pastinaca sativa</i> ( <i>n</i> = 8)	23 (12–27) [8–29]	2.8 (2.7–2.9) [2.3–3.0]	200 (156–319) [123–394]	12.5 (10.0–14.7) [5.2–20.1]
<i>Peucedanum palustre</i> ( <i>n</i> = 6)	15 (10–23) [7–35]	2.5 ** (1.0–2.8) [0.3–2.9]	105 (28–189) [5–327]	6.6 ** (2.8–9.2) [0.7–9.3]
<i>Chaerophyllum aureum</i> ( <i>n</i> = 6)	10 (9–10) [5–20]	1.6 ** (1.0–2.0) [0.8–3.0]	88 (34–145) [34–180]	10.2 (3.8–12.2) [3.4–14.5]
<i>Apium graveolens</i> ( <i>n</i> = 7)	16 (11–20) [0–35]	2.3 *** (2.0–2.5) [0.0–2.7]	227 (67–345) [0–384]	11.9 (9.2–14.6) [1.8–24.0]
<i>Daucus carota</i> ( <i>n</i> = 10)	17 (10–20) [1–30]	2.5 * (1.9–3.0) [0.0–3.0]	123 (3–161) [0–191]	6.5 *** (1.0–7.9) [0–10.6]

Notes: <sup>1</sup> Medians, quartiles (in round brackets), and range [in square brackets] are given. Significance of the difference from data for control females fed on *H. mantegazzianum* (Kruskal-Wallis test): \* –  $p < 0.05$ ; \*\* –  $p < 0.01$ ; \*\*\* –  $p < 0.001$ .

sons showed that none of the tested plants significantly differed from *H. mantegazzianum*, although in certain cases the median was twice lower. Note that the total fecundity and life duration were extremely

variable even among individuals fed with plants of the same species. The oviposition intensity estimated by the mean number of eggs laid by a female per day was less variable. Possibly, that is why the dependence of

**Table 4.** Food plant species influence on *Nastus fausti* females oviposition and larvae development on living plants in a greenhouse<sup>1</sup>

Plant species	Type of test				Relative deviation of the measured width of the head capsule from the regression calculated for larvae developed on <i>Heracleum mantegazzianum</i>
	adult oviposition		1st instar larvae transfer		
	results of test				
	positive	negative	positive	negative	
<i>Heracleum mantegazzianum</i>	4	1	10	4	
<i>Heracleum sosnowskyi</i>			3	1	+ 22%, <i>n</i> = 35 ***
<i>Heracleum sibiricum</i>	2	1	4	0	- 7%, <i>n</i> = 14
<i>Heracleum asperum</i>	3	0	2	0	+ 3%, <i>n</i> = 14
<i>Angelica purpurascens</i>	1	2	3	2	- 21%, <i>n</i> = 3
<i>Angelica sylvestris</i>	1	2	0	2	+ 2%, <i>n</i> = 3
<i>Angelica litoralis</i>	2	1	3	0	+ 21%, <i>n</i> = 7
<i>Pastinaca sativa</i>	1	2	6	1	+ 1%, <i>n</i> = 16
<i>Peucedanum palustre</i>	0	4	1	2	
<i>Chaerophyllum aureum</i>	1	2	2	1	+ 1%, <i>n</i> = 8
<i>Apium graveolens</i>	2	1	3	1	- 2%, <i>n</i> = 19
<i>Daucus carota</i>	2	1	4	0	+ 16%, <i>n</i> = 25
Total for all plants (excluding <i>H. mantegazzianum</i> )	15	16	41	14	+ 5%, <i>n</i> = 144

Notes: <sup>1</sup> Numbers of plants with positive and negative results are given (see Material and methods). Empty cells mean no data. For the relative deviation of larval head capsule width from regression calculated for larvae developed on *Heracleum mantegazzianum*, median percent, sample size, and significance of the difference (Kruskal-Wallis test: \*\*\* -  $p < 0.001$ ) are given.

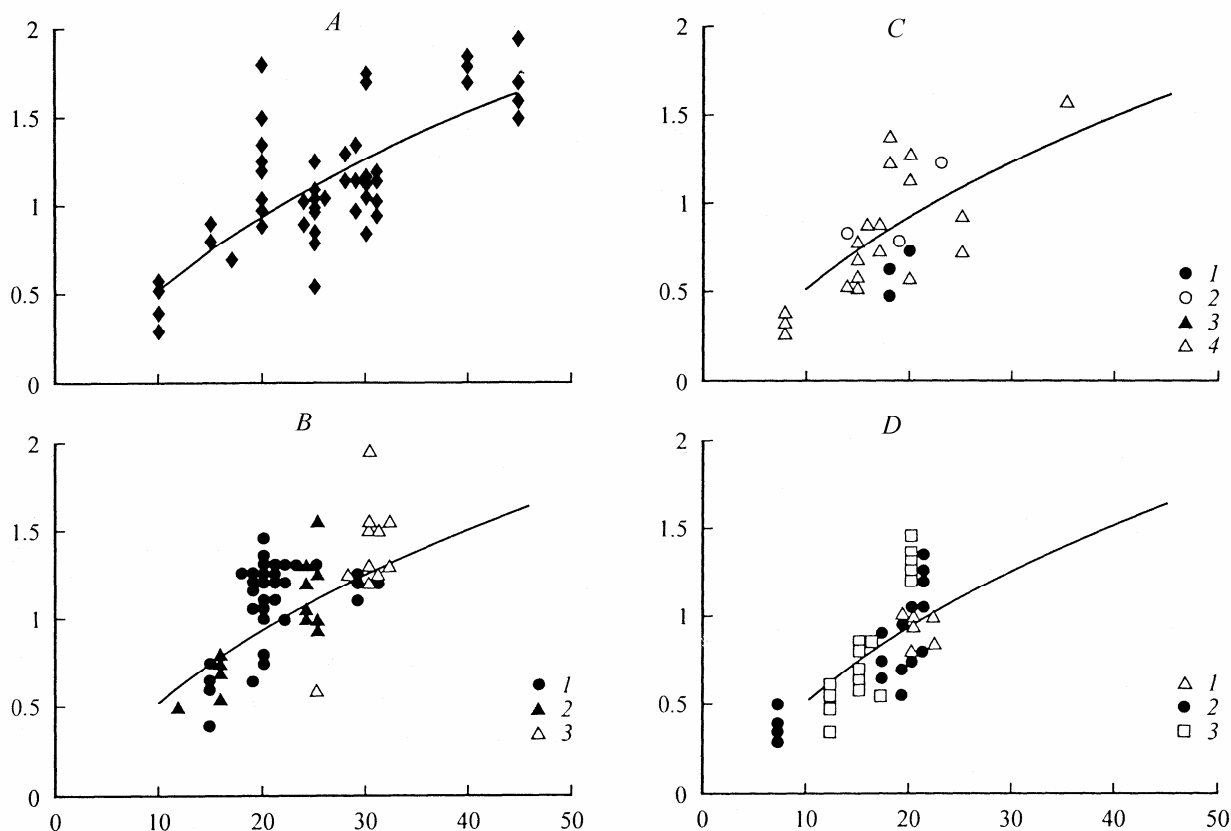
this parameter on the food plant was more significant ( $p = 0.003$ ), and the paired difference was significant for two of the tested plant species. However, even in these cases nothing more than a twofold difference in oviposition intensity was recorded (Table 3).

**Oviposition of females and larval development on potted plants.** Living larvae or obvious traces of their feeding were recorded in experiments with each tested plant species, excluding *Peucedanum palustre* (Table 4, left part). The number of tested plants of each species was too small for paired comparison, but subtotals for *Heracleum* species (82% positive,  $n = 11$ ) and for other plants (30% positive,  $n = 20$ ) were significantly different ( $\chi^2 = 7.6$ ,  $p < 0.01$ ). This suggests that species of the genus *Heracleum* are either more suitable for oogenesis of females, or more often provoke oviposition, or provide better food for the larvae of *N. fausti*. The first and the second hypotheses do not agree with the results of the previous test: when females were placed in Petri dishes, both total fecundity and oviposition intensity were practically equal in females feeding on plants of *Heracleum*

species and on most other tested plants. To check the latter hypothesis, the following experiment was conducted.

**Growth and development of 1st instar larvae transferred onto potted plants.** The results of this test are given in the right part of Table 4. As in the previous experiment, at least one positive result was obtained from each tested plant species. Moreover, the subtotal for *Heracleum* species (79% positive,  $n = 24$ ) was practically the same ( $\chi^2 = 0.5$ ,  $p \approx 0.5$ ) as the subtotal for other plants (71% positive,  $n = 31$ ).

Although in the roots of some test plants only traces of larval feeding were recorded, in most cases, living larvae were also collected. To estimate the rate of their growth and development, the width of the head capsule was measured. As should be expected, the average size of larvae increased in the course of the experiment. In control larvae developing on the roots of *H. mantegazzianum*, the correlation between the width of the head capsule (mm) and the age of the larva



**Fig. 1.** Interrelations between age and size in *Nastus fausti* larvae developed on different plant species. Abscissa: age (days), ordinate: head capsule width (mm). Regression line was calculated for larvae developed on in *Heracleum mantegazzianum*, symbols indicate data for individual larvae developed on: (A) *H. mantegazzianum*; (B) *H. sosnowskyi* (1), *H. sibiricum* (2), *H. asperum* (3); (C) *Angelica purpurascens* (1), *A. sylvestris* (2), *A. litoralis* (3), *Apium graveolens* (4); (D) *Chaerophyllum aureum* (1), *Daucus carota* (2), *Pastinaca sativa* (3).

(days) could be rather well ( $r = 0.73$ ,  $n = 48$ ) approximated with the formula  $Y = -9.4 + 6.3 X^{1/2}$ .

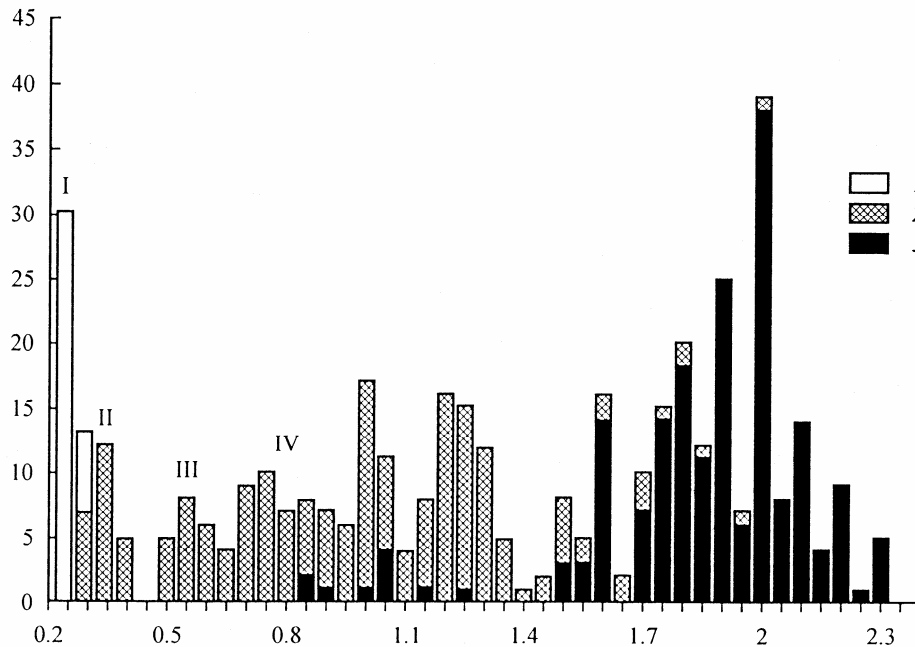
The high variation (Fig. 1A) may be partly explained by non-synchronous larval moults. Data on interrelations between larval age and size received for individuals developing on roots of other plant species agree well with the same regression (Figs. 1B–1D). The relative difference between the experiment (the size of larvae which developed on a tested plant) and the prognosis (regression, i.e. the average size of larvae of the same age which developed on *H. mantegazzianum*) was calculated with the formula  $D = 100 (S - R) / R$ , where  $D$  is relative difference (%);  $S$  is the measured width of the head capsule,  $R$  is the width of the head capsule calculated with the regression formula.

In total, larvae which developed on *H. mantegazzianum* were even slightly smaller than even-aged individuals which developed on other plant species: the average relative difference (median and quartiles)

was +5% (from -10% to +27%), although this difference was not significant ( $p = 0.17$ ,  $n = 144$ , Kruskal-Wallis test). Data for each tested plant species are given in Table 4. It can be seen that the difference between the measured and predicted size was statistically significant only for *H. sosnowskyi*: larvae which developed on this plant were slightly larger than controls (see also Fig. 1B).

The data we have (Fig. 2) are not sufficient for an exact estimation of the number of *N. fausti* larval instars by the size distribution pattern. However, considering that the size of the head capsule in hatching larvae of the 1st instar is 0.25–0.30 mm, it seems (Figs. 1, 2) that under greenhouse conditions the first moult takes place before the 10th day, the second moult, between the 10th and the 20th day, and the third moult, between the 20th and the 30 day of larval life. From the literature (Mashchenko, 1975) it is known that the species from the same Entiminae subfamily, *Otiorynchus asphaltinus* Germar, has 7 larval





**Fig. 2.** Size distribution pattern of *Nastus fausti* larvae. Abscissa—head capsule width (mm), ordinate—number of larvae (total  $n = 421$ ); 1, neonate larvae of the 1st instar ( $n = 36$ ); 2, larvae reared in laboratory ( $n = 192$ ); 3, larvae collected under natural conditions ( $n = 193$ ). Roman numbers indicate estimated larval instars.

instars. Possibly, such a high number of larval instars is also the case for *N. fausti* (Fig. 2). The relative rarity of older instars under laboratory conditions could be explained by overpopulation: roots of many tested plants were completely destroyed by the larvae. Under natural conditions, on the contrary, it is very difficult to count younger larval instars. Anyway, from Fig. 2 it is clear that the width of the head capsule of the last larval instar was ca 2 mm, as such large larvae were collected in September under natural conditions, together with pupae and teneral adults (Table 1). Under laboratory conditions, larvae of this size were found only on *Heracleum* species (Figs. 1A–1B). However, in some larvae which fed on other host plants the head width exceeded 1.5 mm, suggesting successful development at least to the last but one instar.

**Host specificity under natural conditions.** These studies were conducted in Gubskaya environs (Table 1, population no. 9a). Host specificity was estimated by collection of larvae and adults from *H. mantegazzianum* and from *Angelica purpurascens*, which naturally grows in the same habitats, a few meters next to giant hogweed plants. Note that preliminary studies showed that *A. purpurascens* was suitable for *N. fausti* larval and adult feeding under laboratory conditions (Fig. 1C; Tables 3, 4).

Adults were collected in spring, soon after reactivation. In total, 170 adults were collected from *H. mantegazzianum* and 26 beetles were found on *A. purpurascens*. This proportion was close to the visually estimated relative abundance of these two plant species in the studied locations. Obviously, these results could be considered as rough estimation of adult feeding selectivity, as adults were very active and could freely move between plants.

Quantitative sampling of larvae gave much more convincing results. Larvae were collected in autumn (16.09.2007) when most of them intensively fed on roots before hibernation or pupation. Roots of 10 plants of each species and the soil in close vicinity to the roots were carefully inspected. Each inspected *H. mantegazzianum* plant was populated by weevils. In total, 37 larvae, 9 pupae, and 1 teneral adult were found. Median and quartiles were 3.5 (2–8) individuals / plant, which was rather close to the data obtained in September 2005: 183 individuals per 51 plants (Table 1). *A. purpurascens* plants were much less densely populated by weevils: on 10 plants, only 10 larvae and 7 pupae were found, median and quartiles were 1 (0–1) individuals / plant. However, 7 of 10 sampled plants were infested by *N. faustit*. Obviously, under natural conditions *A. purpurascens* is also an acceptable, although not preferred host plant.

We conclude that under laboratory conditions *N. fausti* larvae and adults are able to feed not only on giant hogweeds, but also on a number of other Apiaceae plants, including such important cultivated species as carrot, parsnip, and celeriac. Feeding on some of these plants did not cause significant decrease in female fecundity and did not slow down larval growth and development. Moreover, *N. fausti* adults and larvae feeding on *Angelica purpurascens* were also recorded under natural conditions. Thus *N. fausti* could be considered an oligophagous species connected with plants from at least several genera of Apiaceae.

On the other hand, *N. fausti* was never recorded as an insect pest of carrot, parsnip or other apiaceans, although this weevil is very abundant in giant hogweed populations located on the periphery of villages, in close vicinity of vegetable gardens. Under laboratory conditions, a significant difference between tests conducted with *Heracleum* species and other plants was found in experiments on ovipositing females, but not in those on the 1st instar larvae transfer. In aggregate, these data suggest that it was the selective behavior of ovipositing females which made the natural host specificity of this weevil much narrower than that recorded in no-choice tests conducted in laboratory conditions.

Some authors (Wan and Harris, 1997; Dernovici et al., 2006) believe that it is possible to introduce phytophagous insects which are able to feed on cultivated crops or on autochthonous wild plants providing that these plant species are less suitable for insect development and less preferred by ovipositing females. However, this potentially wide host specificity, together with behavioral modifications and genetic variability is considered by the majority of researchers as one of the most serious risks connected with the introduction of phytophagous insects for classical biological control of weeds (Withers, 1999; McFadyen and Weggler, 2000; Heard, 2000; Tallamy, 2000; Withers et al., 2000; Gassmann et al., 2006; Sheppard et al., 2006). With regard to this fact, based on the results of our study, we conclude that the weevil *N. fausti* cannot be considered a potential agent for biological control of invasive giant hogweeds.

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