

Striking Differences in Behaviour and Ecology Between Populations of *Chrysomela lapponica*¹

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Abstract. Willows and poplars have been suggested as ancestral host plants of *Chrysomela* species (Coleoptera, Chrysomelidae). In the leaf beetle species *C. lapponica*, some populations are specialized on willow species, but others on birch. In this paper, we review results from previous studies on ecological interactions between *C. lapponica* and its biotic and abiotic environment. We found striking differences between individuals of different populations in morphological traits, chemical composition and origin of larval glandular secretions, feeding habits, host preferences and feeding stimulants of larvae and adults. Furthermore, we discovered significant between-population differences in bottom-up, host plant depending performance parameters such as developmental time, body mass, and mortality as well as differences in top-down effects such as defensive secretions against predators, parasitoids and pathogens. We review results of hybridization experiments between different populations and then address the question whether the different host-specific populations of *C. lapponica* represent more than one species.

Key words. Speciation, post zygotic isolation, host shift, larval defence, top-down effect, bottom-up effect, willow, birch, *Chrysomela lapponica*

1. INTRODUCTION

Leaf beetle species belonging to the *Chrysomela interrupta*-group, a subtaxon of the Chrysomelina, show variation in host plant specialization. Some species are specialized to feed and oviposit on willows (Salicaceae), while others live only on birch or alder (Betulaceae) (BROWN 1956; GROSS 1997; GROSS et al. 2004b; GROSS & HILKER 1995; TERMONIA et al. 2001; TERMONIA & PASTEELS 1999). Among the *C. interrupta*-group, populations of *C. lapponica* are known to be exclusively specialized on either birch or on willow. *Chrysomela lapponica* is distributed almost continuously in Northern Europe (e.g., Finland, Sweden, Norway, Russia, Baltic States) (GROSS 2001; GROSS et al. 2004b; HILKER & SCHULZ 1994; MACHKOUR M'RABET 1996; ZVEREVA et al. 1995) and is divided by the boreal coniferous forest belt from the populations in Central Europe, which are distributed patchily in mostly higher or colder regions such as Germany, Czech Republic, Poland, Northern Italy and France (GROSS 1997; GROSS et al. 2004c; HILKER & SCHULZ 1994). The larvae and adults from Northern Europe feed and oviposit only on some willow species, while most of the Central European populations are monophagous on birch (GROSS 1997; GROSS & HILKER 1995). The aim of this review is to summarize information about the ecological factors, which may have driven the divergent evolution of host plant spe-

cialization in the Northern and Central European populations of *C. lapponica*. To elucidate this matter, we compared two populations of *C. lapponica*, which are specialized on different host plants. One of the populations occurs in Finnish Lapland and feeds mainly on the willow *Salix borealis*. The other population, feeding exclusively upon the birch *Betula pubescens*, was observed in the Czech Republic, close to the city of Mariánské Lázně. Both, birch and willow hosts occur sympatrically in the habitats of the Finnish and Czech beetles. We conducted field and laboratory investigations over nine years, using morphological, chemical, physiological and microbiological analyses to determine whether or not these host specialized populations were one and the same species.

2. OVERVIEW OF PRESENT RESULTS

2.1. Morphological differences

The adults of birch-feeding populations of *C. lapponica* differ in the colour patterns of their red and black elytra compared with their willow-feeding counterparts from Northern Europe and Central Europe. While the ratio of black and red colour is about fifty-fifty in the Czech population, the relative size of the black marks of the Finnish beetles' elytra is significantly higher (GROSS et al. 2004c). The tibiae of the adults' first leg pair of the Czech population are predominantly black coloured, whereas the tibiae of the Finnish beetles are mainly red. Sometimes complete blue morphs occur spontaneously

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within the populations of Central Europe, but never in the populations from Northern Europe.

The larvae of the *Chrysomelina* and *Phyllodectina* possess nine pairs of dorsolateral defensive glands located on thorax and abdomen. When disturbed, the glandular reservoirs can be everted, and subsequently be inverted with the help of specialized retractor muscles. The reservoirs are filled with volatile compounds (GARB 1915; HINTON 1951). However, there are striking chemical differences between the Czech (birch-feeding) and Finnish (willow-feeding) populations of *C. lapponica* in the chemical composition of these larval secretions. Gas chromatography coupled with mass spectrometry (GC-MS) was used to identify the composition of the larval secretions and to quantify their amounts. The secretion of the birch-feeding larvae from the Czech population contained carboxylic acids and carbonic acid esters (Fig. 1A) which were synthesized *de novo* and esterified with alcohols taken from the plant (SCHULZ et al. 1997). However, like in all other willow-feeding *Chrysomela*-species, the secretion of the willow-feeding larvae from Finland contained salicylaldehyde as the major component (Fig. 1B). In all systems studied to date, salicylaldehyde is derived from salicin uptaken from willow leaves by the larvae (GROSS 1997; GROSS et al. 2002; GROSS & HILKER 1995; PASTEELS et al. 1988). Interestingly, the two *C. lapponica* secretion types can easily be distinguished in the field according to their different odours. The secretion of the willow-feeders smells like fruit salad, while the birch-feeder's secretion smells like almond liqueur.

2.2. Ecological interactions

First, we investigated the bottom-up effects, which are influenced by the first trophic level, the host plants. To assess these effects, we used different parameters for measuring the performance of the beetles on different plants. These were mortality, developmental time, volume of the larval secretion, fecundity and body weight of the neonate larvae and adults. Secondly, we investigated the top-down effects, that is, those influenced by the third trophic level, like predators, parasitoids and pathogens. An interspecific competition (within the 2nd trophic level) could not be detected (GROSS 2001).

Bottom-up effects. The adults of both Finnish and Czech populations prefer their natural host plant for feeding and oviposition over that of the host plant of the other population (GROSS & HILKER 1995). While there was neither a difference in fecundity nor in body weight of neonate larvae, we observed significant differences in mortality when the beetles were reared on their natural host plant versus the host plant of the other population without enemies in the laboratory (GROSS et al. 2004a). While a few individuals of the birch-specialized popula-

tion could be reared on willow, all neonate larvae of the willow-specialized population died after having been transferred to birch (GROSS et al. 2004a). When individuals of the two *C. lapponica* populations were reared on their natural host plants, the birch specialists suffered higher mortality than the willow specialists (GROSS et al. 2004a). Probably as a consequence of host plant specialization in *C. lapponica*, there was a significantly shorter developmental period for the Finnish beetles on willow compared to that of the Czech beetles feeding upon birch (GROSS et al. 2004a). If the "slow-growth, high-mortality" hypothesis (WILLIAMS 1999; DENNO et al. 1990) applies to *C. lapponica*, the prolonged developmental time might be detrimental to the birch-feeding larvae, because they would remain in the more vulnerable larval stages for a longer time period. Higher mortality could result from higher predation, parasitism or higher microbial infection rates. Fecundity does not differ between individuals of both populations. However, a smaller volume of larval secretion is produced by the birch-feeding larvae (GROSS et al. 2004a).

Top-down effects. Laboratory experiments showed that both types of larval secretions (above-mentioned) of *C. lapponica* are highly effective against generalist predators with chewing-biting mouthparts like coccinellids, but ineffective against generalists with sucking-piercing mouthparts (GROSS 2001). However, significant differences exist between both secretion types in the effectiveness towards pathogens. The secretion of the willow-feeding larvae was highly effective against various microorganisms, especially against the entomopathogenic fungus *Metarhizium anisopliae*. When applied directly onto the blastospores, fungal germination and growth was greatly inhibited by the main component of the secretion, salicylaldehyde. Additionally, physiological quantities of volatile salicylaldehyde were shown to reduce germination and growth of *M. anisopliae* up to 45 mm around the application site (GROSS et al. 2002). In contrast, no antimicrobial activity was found in the larval secretion of the birch-feeding population. Laboratory results supported field observations because no infected ontogenetic stages of *C. lapponica* were found in Finland, while infected larvae and pupae were collected in the Czech Republic (GROSS 2001).

It was previously known that salicylaldehyde, the main component of the secretion of willow-feeding larvae, did not repel but instead attracted a specialized enemy, the predaceous hoverfly *Parasyrphus nigrivittatus* (KÖPF et al. 1997). Therefore, laboratory studies were conducted to evaluate the response of *P. nigrivittatus* larvae towards the salicylaldehyde-free secretion of the birch-feeding larvae. *Parasyrphus nigrivittatus* hunted for larvae of both populations, but the secretion of the birch-feeding larvae was significantly less attractive than that of the willow-feeding larvae. Faeces of the willow-

feeding larvae attracted this predator, as well. However, *P. nigratarsis* did not respond to faeces of larvae fed with birch leaves. In the field, *P. nigratarsis* is common in both habitats, but infested egg batches were found only on willows. The hover fly was never observed preying on individuals of the birch-feeding population (GROSS et al. 2004b).

In general, a higher percentage of the willow-specialized *C. lapponica* were found to be parasitized compared with the birch specialists. Both, in 1999 and in 2000, the percentage of parasitization by the phorid fly *Megaselia opacicornis* of the willow-specialized *C. lapponica* specimens was significantly higher than of the birch specialists. This parasitoid cannot be repelled by larval secretions. Parasitization by other species was low in each year both for birch and willow specialists (GROSS et al. 2004b). The parasitoids that were reared from parasitized *C. lapponica* larvae or pupae are all known to only develop in *Chrysomela* species (COX 1994; DISNEY et al. 2001; ZVEREVA & KOZLOV 2000). The influence of host plants or larval secretions on the host-finding behaviour of parasitoids was tested in field experiments in Finland. These experiments showed that parasitoids use both chemical signals of the willows (GROSS et al. 2004b) and volatile secretions of the willow-feeding larvae as kairomones for host localization (ZVEREVA & RANK 2004).

Abiotic factors (e.g., temperature, radiation). The adaptive value of the elytral colouring, one of the most conspicuous differences between the adults of both populations of *C. lapponica*, was examined. Adults of the Finnish and other populations from Northern Europe were found to be significantly darker in colour than their Czech counterparts (GROSS 1997; GROSS et al. 2004c; ZVEREVA et al. 2003). As a result, Finnish beetles heated up more quickly when exposed to insolation. The dark colouring of the Finnish beetles may therefore be an adaptation to their colder environment with shorter seasonal vegetation periods (GROSS et al. 2004c). Also, some endogenous factors were found to differ between the populations. Batch calorimetry experiments gave evidence that the specific metabolic rate during hibernation at low temperatures was lower in the Czech beetles. Individuals of the Czech population may have to cope with higher and fluctuating winter temperatures. Additionally, the walking speed and the feeding activities of the Finnish beetles were higher at low temperatures when compared to the Czech beetles (GROSS et al. 2004c).

Crossing experiments. Very few examples of host race formations are known in chrysomelids. Among them are the *Gallerucella nymphaeae* species complex (HIPPA & KOPONEN 1986; NOKKALA & NOKKALA 1994; NOKKALA & NOKKALA 1998; PAPPERS et al. 2002b; PAPPERS

et al. 2002a) and the *Lochmaea caprea* (Kreslavskiy & Mikheyev 1994). However, unconfined hybrid formation was possible between the host races in these examples. Fatouros et al. (unpublished results) tried to interbreed individuals of *C. lapponica* from Finland (willow-feeders) and the Czech Republic (birch-feeders) in the laboratory. Only a unidirectional hybrid formation between females from the Czech Republic and males from Finland succeeded, whereas the reciprocal pairings produced no offspring. But the resulting hybrid larvae could not survive. By keeping the ability to feed on only willow, they were doomed to death on birch, as their birch-feeding mothers laid the eggs exclusively on birch leaves. This represents possibly a new postzygotic isolation mechanism (Fatouros et al. in press).

3. DISCUSSION

This review focuses on the ecological factors which selectively influence phenotypically different individuals of *C. lapponica*. But natural selection is only one of several factors driving the evolution of organisms (MAYR 1997). Other random evolutionary factors like genetic drift and mutation were not investigated.

Influence of biotic selection factors. The influence of biotic selection factors on the two investigated populations of *C. lapponica* is summarized in Table 1. No competition between *C. lapponica* and other herbivores could be detected in both habitats and upon both host plants (GROSS 2001). The respective host plant species had an effect on the performance of the leaf beetle. Birch-feeding larvae feeding under standardized conditions on leaves of their natural host plant, *B. pubescens*, developed more slowly than willow-feeding larvae reared on leaves of their natural host plant, *S. borealis* (GROSS et al. 2004a). This laboratory result, however, may not be of ecological significance, because developmental time increases with higher temperatures (HONÉK & KOCOUREK 1988; HOWE 1967). Therefore the adverse effect of the birch on the beetles' developmental time could be compensated for, since the mean temperatures during the vegetation period in the Czech Republic were significantly higher than in Finland (GROSS et al. 2004c). If this is not the case, the prolonged developmental time might be detrimental to the birch-feeding larvae, because they remain in vulnerable immature stages for a longer period of time. Higher mortality could result from enhanced predation, parasitization or microbial infection (HÄGGSTRÖM & LARSSON 1995; WILLIAMS 1999).

Birch-feeding larvae were also found to have reduced volumes of secretions. This had obviously no effect on the larvae, because even little quantities of secretion were highly effective against ladybird beetles (GROSS et al. 2004a). Apart from directly affecting the beetles de-

velopment and larval secretion quantity, the host plant may also have an indirect influence on top-down effects by determining the chemical composition of the larval defence secretions. A laboratory experiment showed that willow-feeding larvae were better defended against pathogens than birch-feeding larvae due to the salicylaldehyde in the secretion of the willow-feeding larvae (GROSS et al. 2002).

Although birch-feeding larvae seem to face a number of disadvantages as a result of feeding on an apparently suboptimal host, there is evidence for a trade-off: the secretion of birch feeding larvae was shown to be less attractive to the specialist predator, *P. nigratarsis*, than the salicylaldehyde-containing secretion of larvae of the willow feeding populations (GROSS et al. 2004b). Consequently, our data suggest that the secretion of the birch-feeding larvae provides a selective advantage, due to a decreased predation pressure by specialists on eggs and larvae.

Influence of abiotic selection factors. Individuals of *C. lapponica* in Finland and the Czech Republic live in environments, which differ in their temperature conditions and in the length of their vegetation period. Those adult beetles living in colder environments (Finland) benefit from their darker elytral colouring by heating up more rapidly. The higher body temperatures attained positively affect their walking and feeding behaviour (GROSS et al. 2004c). Additionally, their temperature range for feeding and walking activity is lower than in their counterparts living in warmer environments (Czech Republic). In contrast, the lower specific metabolic rates of the Czech beetles at low temperatures are favourable during hibernation, because their energy resources decrease more slowly than the energy resources of the Finnish beetles. The elytral colouring as well as internal physiological factors lead to an optimal adaptation to temperature conditions in the different habitats of *C. lapponica* in Central and Northern Europe (GROSS et al. 2004c).

Summarizing the effects of the three trophic levels on *C. lapponica*, plant (i.e., host plant species), herbivorous insect (i.e., competitors), and antagonists (i.e., predators, parasitoids, and pathogens), the following evolutionary scenario arises. Since larvae adapted to willow have a shorter developmental period if reared on willow than birch-feeders reared on birch, willow is obviously a better food plant than birch. Competition between *C. lapponica* and other herbivores could not be detected. Consequently food does not seem to be limiting. Feeding on willow benefits larvae due to the antimicrobial activity of their willow-derived salicylaldehyde-rich secretion. The secretion protects willow-feeding larvae against fungal infection. Birch-feeding larvae are more vulnerable to fungal infections since their secretion lacks sig-

nificant antifungal activity. Nevertheless, feeding on birch has a major advantage as it allows those larvae to produce a secretion which is significantly less attractive to specialist predators like the hoverfly, *P. nigratarsis*, than the secretion of the willow-feeding larvae. The different elytral colouring and temperature optima traits of the imagoes from both populations appear to be highly adaptive to the extant environmental conditions in their current ranges.

Is the willow the ancestral host plant? The results reviewed here suggest that the ancestral host plant of *C. lapponica* belonged to the Salicaceae: While individuals of the birch-feeding population of *C. lapponica* can obviously cope with the secondary metabolites of the willow, as they are still able to develop from larvae to adults when fed with willow leaves, individuals of the willow-feeding population cannot survive when fed with birch leaves (GROSS et al. 2004a). When reared on *Salix fragilis* in the laboratory, birch-feeding larvae produce trace amounts of salicylaldehyde in their secretion (GROSS 1997; HILKER & SCHULZ 1994), suggesting that this ability could be a vestige of the ancestral pathway. These findings indicate that the birch-feeding population has adapted very well to its new host-plant in the interim, because its performance is negatively affected when reared on willows (GROSS et al. 2004a). Further studies of the natural enemies of the Nearctic species within the *C. interrupta*-group feeding upon alder have to be conducted in order to elucidate the convergent or reversal host shifts between Betulaceae and Salicaceae, as it was suggested by TERMONIA et al. (2001).

Do the birch feeding populations represent a host race or a new species? According to our findings obtained over the past nine years of field and laboratory experimentation, we conclude that the pronounced and consistent differences in morphology, ecology and ethology between most birch-feeding and willow-feeding populations of *C. lapponica*, the species *C. lapponica* should be divided in two distinct species. With regard to ecologically important traits like feeding specialization and oviposition behaviour, one may distinguish between a birch-feeding species, to which most of the investigated populations from Central Europe belong (Germany, Czech Republic, Poland and France (Massif Central)), and a willow-feeding species, which includes all populations from Northern Europe (Finland, Norway, Russia) and one population from France (Queyras).

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