

# Distribution of race-specific resistance against *Bremia lactucae* in natural populations of *Lactuca serriola*

Irena Petrželová · Aleš Lebeda

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**Abstract** A metapopulation approach was applied to population studies of a common weed, *Lactuca serriola* (prickly lettuce). Seedlings grown from seed samples collected from 752 individual *L. serriola* plants in 50 populations occurring along an east-to-west transect across four European countries (Czech Republic, Germany, Netherlands and United Kingdom) were screened for resistance to 10 common races of *Bremia lactucae*. Based on the recorded reaction patterns, host individuals were characterized into specific resistance (R-) phenotypes. Diversity of R-phenotypes, their variation and distribution among and within European populations, was evaluated at different spatial scales, i.e. from a metapopulation involving the entire European study area to individual plants occurring in local populations. Generally, European populations of *L. serriola* have been shown to be highly susceptible to *B. lactucae*. However, large variation in *L. serriola* resistance was found both among and within individual countries. There was a clear gradient of increasing uniformity of race-specificity moving from central to western Europe, as well as a slight decrease in the diversity of R-phenotypes. Populations in the United Kingdom were the most divergent in terms of resistance structure from other geographic regions, and also were the most homogeneous, most likely a consequence of the relatively greater degree of spatial

isolation from other regions. Metapopulation, inter- and intra-population variation in host resistance is discussed from the viewpoint of occurrence of race-specific interactions in this wild plant pathosystem.

**Keywords** Resistance complexity · Gene flow · Diversity · Host-pathogen interactions · Intra-population variation · Lettuce downy mildew · Metapopulation · Prickly lettuce · Resistance structure

## Introduction

It is well known that pathogens have the potential to play a substantial role in shaping the structure, as well as the dynamics and evolution of natural plant communities (e.g. Burdon et al. 2006). Importantly, studies of wild plant pathosystems have been found to be attractive from an applied perspective, particularly with regard to quantifying factors that determine the evolution and maintenance of variation in host resistance and pathogen virulence. They can yield much information useful for both resistance breeding and the practical management of plant disease (Lenné and Wood 1991; Lebeda et al. 2007b, 2009a). However, the number of wild plant-pathogen associations that have been studied so far is still limited, and there are large differences in the level of available information for individual interactions.

The most intensively studied natural plant-pathogen interaction is that involving *Linum marginale-Melampsora lini*. Many papers have been written concerning various aspects of the host plant-pathogen

I. Petrželová · A. Lebeda (✉)  
Faculty of Science, Department of Botany,  
Palacký University in Olomouc,  
Šlechtitelů 11,  
783 71 Olomouc, Czech Republic  
e-mail: ales.lebeda@upol.cz

relationship (coevolution, spatial and temporal variation, as well as population dynamics and epidemiology) in that pathosystem (e.g. Burdon and Jarosz 1991; Burdon 1994; Burdon and Thompson 1995; Burdon et al. 1999; Burdon and Thrall 1999, 2000; Thrall et al. 2001, 2002). Some additional population studies have been published for other wild plant pathosystems, e.g. *Filipendula ulmaria*-*Triphragmium ulmariae* (Ericson et al. 2002; Smith et al. 2003); *Plantago lanceolata*-*Podospheera plantaginis* (Laine 2004, 2005; Laine and Hanski 2006; Laine 2007); *Senecio vulgaris*-*Erysiphe fischeri* (Bevan et al. 1993a, b, c); *Silene* spp.-*Ustilago violacea* (*Microbotryum violaceum*) (Thrall and Antonovics 1995; Alexander et al. 1996; Delmotte et al. 1999; Carlsson-Granér and Thrall 2002; Carlsson-Granér 2006); and *Valeriana salina*-*Uromyces valerianae* (Ericson et al. 1999). However, there is a large knowledge gap regarding interactions between weed host plants and oomycetes (Holub 2008; Lebeda et al. 2008), despite the fact that oomycete pathogens represent an important group of species which are common in nature and have a world-wide distribution (Lebeda and Schwinn 1994).

In most published studies focused on wild pathosystems, great emphasis is put on the importance of considering host and pathogen interactions within a metapopulation context, i.e. local populations connected by migration events and gene flow (Burdon 1993; McDermott and McDonald 1993). Regional differences in migration rates may result in large differences and variation among individual local populations but these represent only small pieces of a highly diverse mosaic of resistance and virulence phenotypes over a larger area. Most of the studies mentioned above also highlighted the necessity for parallel studies of the population structure of both participants in interactions between plants and obligate biotrophic pathogens (Clarke and Akhka 2002; Holub 2008; Lebeda et al. 2008), especially because their populations are, of necessity, closely interconnected in a coevolutionary sense. Knowledge of populations of one species (either host or pathogen) within these interactions may help to explain much of the behavior of the populations of coevolving species.

In our study we focused on the wild plant pathosystem *Lactuca serriola* L. (prickly lettuce)-*Bremia lactucae* Regel (lettuce downy mildew). *B. lactucae* is an oomycete pathogen of cultivated lettuce (*Lactuca*

*sativa*), as well as many other species of Asteraceae that have worldwide distribution (Lebeda et al. 2002, 2007b). For the 17 *Lactuca* species described from Europe (Lebeda et al. 2001a), only seven are known as natural hosts of *B. lactucae* (Lebeda et al. 2002). Of these seven species, *L. serriola* is the most common wild host of *B. lactucae*, as has recently been published for the Czech Republic (Petrželová and Lebeda 2004a; Lebeda et al. 2007a, 2008) and the Netherlands (Hooftman et al. 2006). In other European countries only sporadic occurrences of natural infections by *B. lactucae* were recorded during collection of *Lactuca* spp. in Austria, France, Germany, Switzerland (Lebeda et al. 2001a) and Slovenia (Doležalová et al. 2001).

Currently, there are no detailed studies focused on the natural distribution of *B. lactucae* in Europe or the other continents. However, we recently acquired a large amount of information for the Czech pathogen populations of *B. lactucae* on the wild host *L. serriola* (Lebeda 2002; Lebeda and Petrželová 2004a; Petrželová and Lebeda 2004b; Lebeda et al. 2008). However, to date there are no corresponding detailed data for resistance variation in Czech host plant populations. The same is true for the host populations in the other European countries (Lebeda et al. 2007a).

The aim of our present research was to: a) screen *L. serriola* samples originating from four European countries for their resistance to 10 isolates of *B. lactucae*; b) determine the diversity of resistance phenotypes, and c) assess both their distribution and variation at the intra- and inter-population levels within the European metapopulation of *L. serriola*. Some partial results had been published previously (Lebeda and Petrželová 2004b, 2007a, b; Lebeda et al. 2008). In this paper we present a more detailed analysis of various aspects of resistance variation within populations of *L. serriola*. Here we summarize the results of this analysis, which includes data from a broad range of different *L. serriola* populations across different geographic regions.

## Materials and methods

### Collection of plant materials

*Lactuca serriola* seed samples used for our research originated mostly from collections made in 2001 as part of the Fifth Framework Programme of the

European Union called “Gene-Mine”. Fifty populations of *L. serriola* occurring in four European countries (Czech Republic (CZ),  $n=16$ ; Germany (D),  $n=16$ ; Netherlands (NL),  $n=8$ ; and United Kingdom (UK),  $n=10$ ) were investigated and seeds collected (Lebeda et al. 2007a). Collection sites were distributed along transects throughout the countries studied in order to collect the most representative samples of the spatial variation of resistance in the European *L. serriola* metapopulation (Fig. 1). In order to capture variation within individual local populations of *L. serriola*, seeds were taken separately from individual plants; if available, 16 plants per population were examined. Summaries of data on the origin of the *L. serriola* samples, including site geographical and ecological characterizations, as well as information on the observed populations of *L. serriola* and the occurrence of natural infections caused by fungal pathogens, have been published elsewhere (Lebeda et al. 2007a). Examples of the most common habitats of *L. serriola* are depicted in Fig. 2. Plants with symptoms of natural infection are shown in Fig. 3.

Plant and pathogen materials used to evaluate resistance patterns

Naturally-growing *L. serriola* plants did not provide enough seed usable for our experiments. The collec-

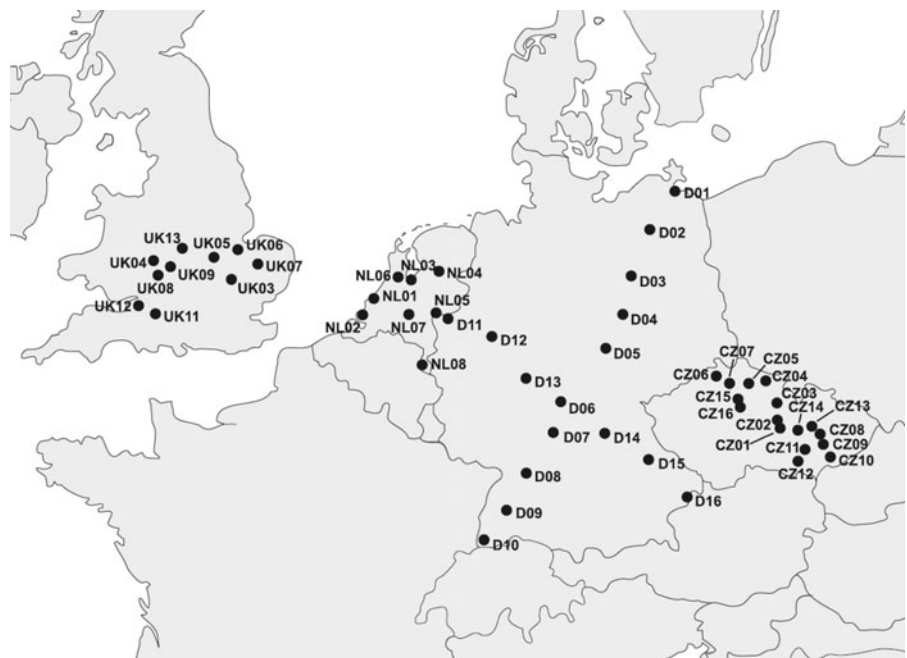
tion samples, originating from individual plants, had to be regenerated and multiplied in a greenhouse first, and the seeds derived from a total of 752 samples were included in resistance screening (Table 1). Thus, in the present study “samples” are considered as the sets of *L. serriola* plants grown from seeds of regenerants derived from original collection samples, and represent original individuals ( $n=752$ ) from the natural populations ( $n=50$ ) of *L. serriola* originally examined (Lebeda et al. 2007a).

*L. serriola* samples were screened for their resistance to 10 isolates representing the officially denominated races of *B. lactucae* Bl:1, Bl:5, Bl:12, Bl:14, Bl:15, Bl:16, Bl:17, Bl:18, Bl:21, and Bl:24 with known virulence patterns (van Etteken and van der Arend 1999; van der Arend et al. 2006). The *B. lactucae* isolates used in this research originated from cultivated lettuce (*Lactuca sativa*) and are maintained in the Czech National Collection of Microorganisms (<http://www.vurv.cz/collections/vurv.exe/>) at Palacký University in Olomouc, Department of Botany (<http://botany.upol.cz>).

Inoculation studies and resistance screening

The tests were carried-out according to the methods described in Lebeda (2002) and Petrželová and Lebeda (2004b). Pathogen races were maintained

**Fig. 1** Collection sites of *Lactuca serriola* populations in the Czech Republic, Germany, Netherlands and United Kingdom (Lebeda et al. 2007a)







**Fig 2** Populations of *Lactuca serriola* in its common habitats, representing the origin of plant material used in this study (examples from the Czech Republic). *L. serriola* is a typical synanthropic species, which occurs as a pioneer plant in the early successional stages of a vegetation, and occupies various man-made habitats; typically, waste areas with disturbed soils (for more details about *L. serriola* habitats see e.g. Lebeda et al. 2001a, 2007a, 2008). Several basic categories (bold text) were

distinguished: along the transport corridors such as railway (see **a**) or ditches and roadsides (**b**); agricultural areas, mostly field roads or field margins (**c**); ruderal areas such as dust heaps (**d**), debris, building sites or man-made piles of soil; urban areas, mostly pavements (**e**), uncultivated lawns (**f**) or parking sites; larger neglected areas (fallows) (**g**); moist habitats such as moist ditches (**h**), or places with a local accumulation of biological material (dunghills or compost-heaps) (**i**)

and multiplied on seedlings of *L. sativa* cv. Cobham Green (R0), which also served as a universally susceptible control. For each *L. serriola* sample tested, ca. 25 seeds were sown. Plants were inoculated at the fully expanded cotyledon leaf stage (usually 7 days after sowing) by spraying with a conidial suspension of a particular *B. lactucae* race. Inoculated seedlings were incubated at 10–15°C, for the first 12–24 h after inoculation in the dark, and thereafter grown under a 12 h day/night photoperiod.

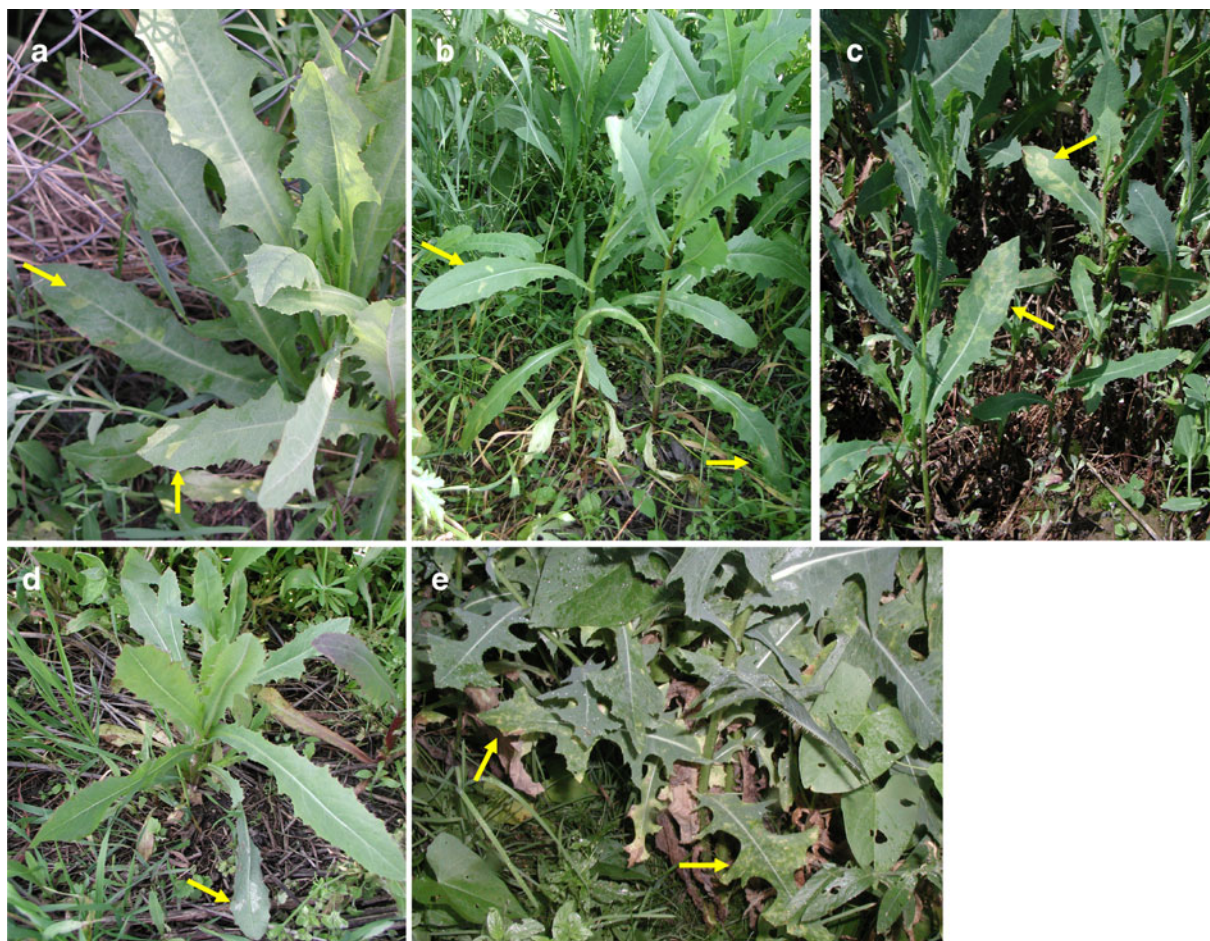
Sporulation intensity was assessed 14 days after inoculation using a 0–3 scale (Dickinson and Crute 1974), and then expressed as a percentage of the

maximum scores, according to Townsend and Heuberger (1943). The reaction of a particular *L. serriola* sample was considered as susceptible if the sporulation intensity was more than 30%, and at least half of the seedlings showed a high degree of infection (i.e. rated 2 and/or 3). Tests giving ambiguous results were repeated.

#### Interpretation of resistance data

The resistance phenotypes (R-phenotypes) of individual *L. serriola* samples were characterized on the basis of the recorded reaction patterns. This data was then used to examine patterns of variation in resistance to





**Fig 3** *Lactuca serriola* plants with symptoms of natural infection by lettuce downy mildew. Weedy growing plants can be infected by *B. lactucae* in all developmental stages (Petrželová and Lebeda 2004a). Typically, *B. lactucae* causes light green, yellow or necrotic lesions surrounded by larger leaf veins, visible on the upper leaf surface (Lebeda et al.

2008). Figure shows the early stage of infection on rosette (a) or stem leaves (b) of the young plants. Sometimes, young plants may be completely covered with lesions (c). Under optimal microclimatic conditions, sporulation occurs on the lower surface of lesions (d). Figure (e) shows strong infection on stem leaves of adult *L. serriola* plants

*B. lactucae* within and between wild populations of *L. serriola*. Variation was assessed at several different spatial scales (European metapopulation, regional populations extended over larger areas of the European countries studied [in the sense of “spatially extended

populations” suggested by Freckleton and Watkinson (2002)], local populations and individuals within populations). Our aim was to assess whether there were any geographic differences in the resistance of *L. serriola* populations, determine spatial patterns of

**Table 1** Survey of *Lactuca serriola* populations and samples screened for resistance

Origin of seed samples	Number of populations	Number of seed samples
Czech Republic (CZ)	16	250
Germany (D)	16	241
Netherlands (NL)	8	120
United Kingdom (UK)	10	141
Totally	50	752

resistance variation, and to evaluate at which spatial scale the variation is most pronounced.

## Results

Evaluation of the resistance of *L. serriola* populations in their natural habitats

As mentioned previously, collecting trips, designed to study weedy populations of *L. serriola*, were undertaken in 2001. Information about the occurrence of diseases on *L. serriola* plants was also recorded (Lebeda et al. 2007a). Surprisingly, the natural occurrence of *B. lactucae* infections in European populations of *L. serriola* was rarely observed within the host European metapopulation. In fact, in 2001, diseased populations of *L. serriola* were only found in the Czech Republic, where the disease incidence was very high. From a total of the sixteen populations that were examined for the presence of *B. lactucae*, fifteen were infected. However, disease prevalence (expressed for the whole local population as the degree of visually observable infection (DI) using the 0–3 scale (Lebeda et al. 2008)) was very low in most populations (two populations displayed a medium level of disease prevalence [DI2], and one a high level [DI3]).

Resistance of European metapopulation of *L. serriola* to *B. lactucae*—a general view

Resistance screening of *L. serriola* samples revealed broad variation in resistance within the European

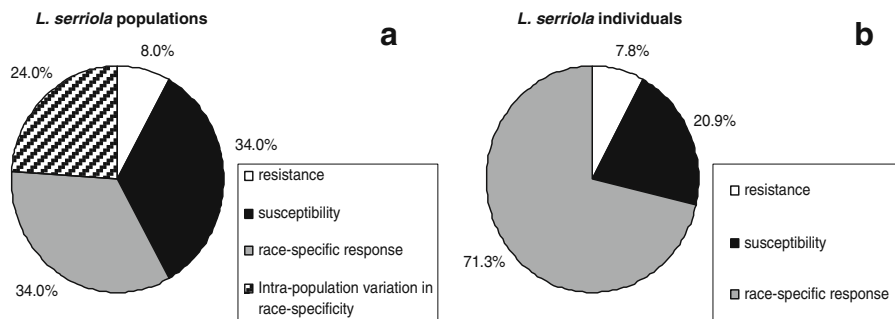
metapopulation, both at the level of populations and of individuals (Fig. 4). The relative resistance of populations of *L. serriola* was assessed, taking into consideration the prevalent reaction patterns of tested *L. serriola* samples to the set of 10 races of *B. lactucae* used. As shown in Fig. 4a, the overall resistance of the European metapopulation was quite low, which is in contrast with only slightly infected or infection-free populations observed during our field trips. Under laboratory conditions, only a few host populations were considered to be resistant; one third of the examined populations were highly susceptible; one third expressed a pronounced race-specific response; and the rest consisted of a mixture of resistant, susceptible, and clearly race-specific responding individuals.

When considering the resistance of the European metapopulation of *L. serriola*, from the viewpoint of the overall resistance of individuals, only 59 samples tested expressed complete resistance to all 10 races of *B. lactucae* used in the inoculation study. In total, 157 samples were susceptible to all races used, and 536 samples expressed more or less pronounced race-specific response (Fig. 4b).

Analysis of resistance variation in *L. serriola* originating from four European countries

*Geographic variation in resistance of L. serriola populations to individual races of B. lactucae*

Despite the overall low resistance of the European *L. serriola* metapopulation, clear differences in resistance to individual races of *B. lactucae* were observed



**Fig. 4** Distribution of resistance to *Bremia lactucae* among *Lactuca serriola* populations ( $n=50$ ) and individuals ( $n=752$ ) within the entire European metapopulation of *L. serriola*. **(a)** Proportion of *L. serriola* populations with a high level of resistance, susceptibility, race-specificity (resistance to several races and susceptibility to other of 10 used races of *B. lactucae*)

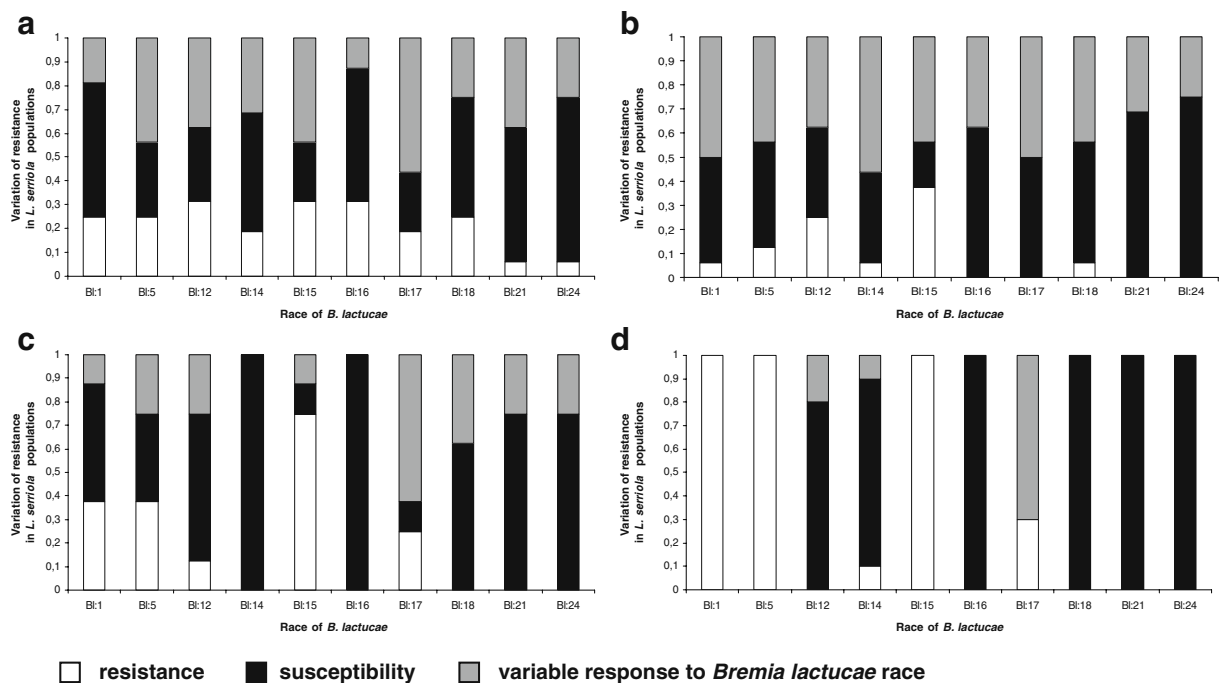
or intra-population variation in resistance (mixture of individuals with highly resistant and highly susceptible reaction patterns occurring in approximately equal ratio within one local population); **(b)** Proportion of *L. serriola* individuals which were completely resistant, completely susceptible or expressed race-specific response to the used set of *B. lactucae* races

among the four countries (Fig. 5). As shown in Fig. 5a, the Czech populations were found to be the most variable in overall resistance to individual pathogen races tested, with respect to both the prevalence of resistant and susceptible responses, and there was also a relatively high frequency of local populations characterized by variable responses of individuals. In Germany (Fig. 5b), overall the prevalence of resistant individuals was lower, and populations were generally either highly susceptible or showed variation in response to individual isolates of *B. lactucae*. Minimal resistance was only recorded for pathogen races Bl:1, Bl:5, Bl:12, Bl:14, Bl:15, and Bl:18. Dutch populations of *L. serriola* (Fig. 5c) were highly susceptible to most of the races used, and only showed high levels of resistance against race Bl:15, with lower levels of resistance to races Bl:1, Bl:5, Bl:12, and Bl:17. Populations in the United Kingdom (Fig. 5d) were characterized by very low variation in their responses. All populations were proven to be completely resistant to pathogen races Bl:1, Bl:5, and Bl:15, and highly susceptible to Bl:12, Bl:14, Bl:16,

Bl:18, Bl:21, and Bl:24. Responses to race Bl:17 were the most variable.

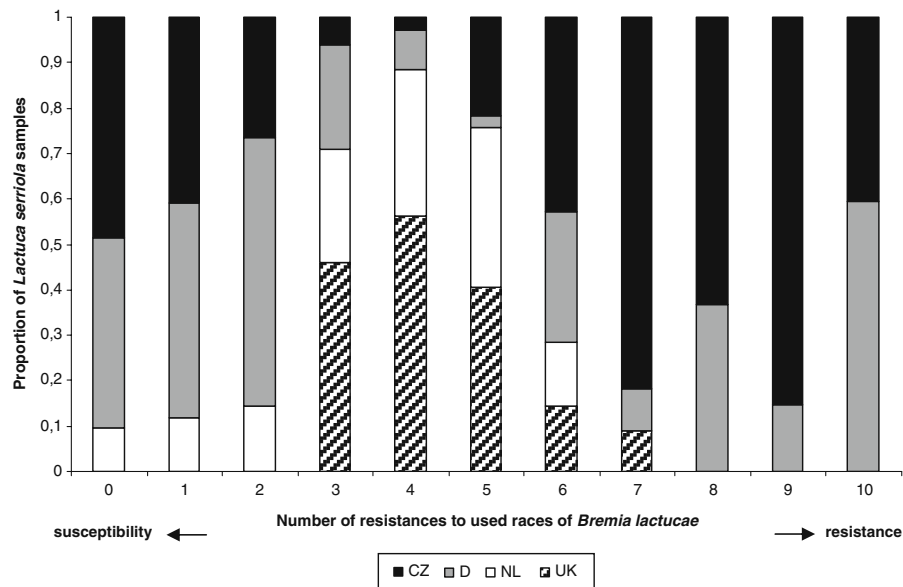
#### *Geographic variation in resistance to the set of B. lactucae races among L. serriola populations and individuals*

A very useful characteristic for the evaluation of resistance of host populations is the complexity of resistance (i.e. the proportion of resistances recorded in a host individual from the total number of resistances examined, in our case from resistances to the 10 pathogen races used), representing the level of race-specificity of the host individuals. The results from the tested *L. serriola* samples from the Czech Republic (CZ), Germany (D), the Netherlands (NL) and United Kingdom (UK) (in our study representing individuals from *L. serriola* populations originally visited) revealed large differences among European countries, with a variety of resistance complexity patterns. Figure 6 shows that individuals with the most complex resistance patterns only occurred in the



**Fig. 5** Variation of resistance of *Lactuca serriola* populations to ten races of *Bremia lactucae* within and among four European countries (**a** Czech Republic,  $n=16$  populations; **b** Germany,  $n=16$ ; **c** Netherlands,  $n=8$ ; **d** United Kingdom,  $n=10$ ). In individual

histograms each column shows a proportion of local populations of *L. serriola* within European country with a prevalence of resistant, susceptible and variable responses (mixture of resistant and susceptible individuals) to individual races of *B. lactucae*



**Fig. 6** Variation in complexity of resistance to the used set of *Bremia lactucae* races ( $n=10$ ) among *Lactuca serriola* populations in four European countries. Complexity of resistance was evaluated for 752 individuals of *L. serriola* and was expressed as

the number of recorded resistant responses of individuals: 0=no resistance to used races of *B. lactucae*, 10=resistance to all races. Each column of the histogram shows a relative proportion of CZ, D, NL and UK samples in the categories 0 to 10

CZ and D regions. However, there were also a large number of individuals found in these countries with a very low complexity of resistance phenotypes, i.e. with low levels of resistances. A completely different situation was found in the NL and UK regions, where individuals generally expressed intermediate levels of resistance complexity, although in the Netherlands some individuals with low levels of resistances were also found (Fig. 6).

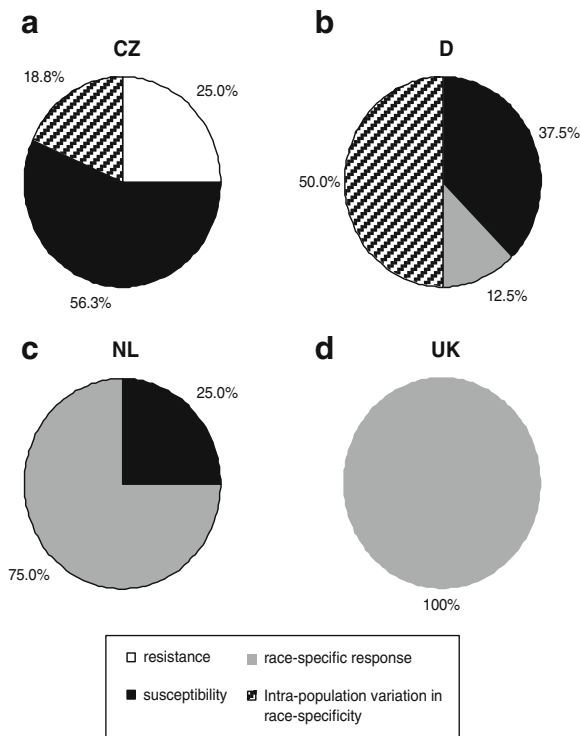
The main goals of our study were to determine the distribution of race-specific resistance among populations of *L. serriola*, and to evaluate whether there are geographical-scale differences in patterns of resistance to *B. lactucae*. The overall resistance of *L. serriola* populations was determined for four European countries, similarly as for the assessment of the resistance of the whole European metapopulation (Fig. 4). We classified local populations of *L. serriola* according to the reaction patterns to the set of 10 races of *B. lactucae* used, (i.e. according to the prevalent level of resistance complexity) (Fig. 7). Our study revealed that race-specific resistance of *L. serriola* was unequally distributed among European regions. Populations with high overall resistance to the set of *B. lactucae* races used were found only in the Czech Republic. However, a large proportion of the CZ

populations expressed high levels of susceptibility or strong intra-population variation in race-specific resistance (Fig. 7a). According to the criteria described above, D populations were among the most variable. More than half of the populations were composed of a mixture of highly resistant and highly susceptible individuals; the rest of the populations were highly susceptible (Fig. 7b). The NL and UK populations studied were highly uniform in their types of responses. The most common reaction pattern recorded was that of pronounced race-specificity (Figs. 7c, d).

At the level of the host individuals, comparison of resistance responses from the four countries showed a slightly different picture for CZ and D than it did at the level of populations. Unlike in the Czech Republic, there were no resistant D populations. However, there was a range of individuals originating from various D populations that expressed a completely resistant response (Figs. 8a, b). The number of resistant individuals was even higher in D populations (total of 35) than in the CZ populations (total of 24). In addition, in both the CZ and D populations there were large numbers of individuals with a relatively pronounced race-specific response.

The graphs showing proportions of resistant, susceptible, and race-specific responsive NL and UK



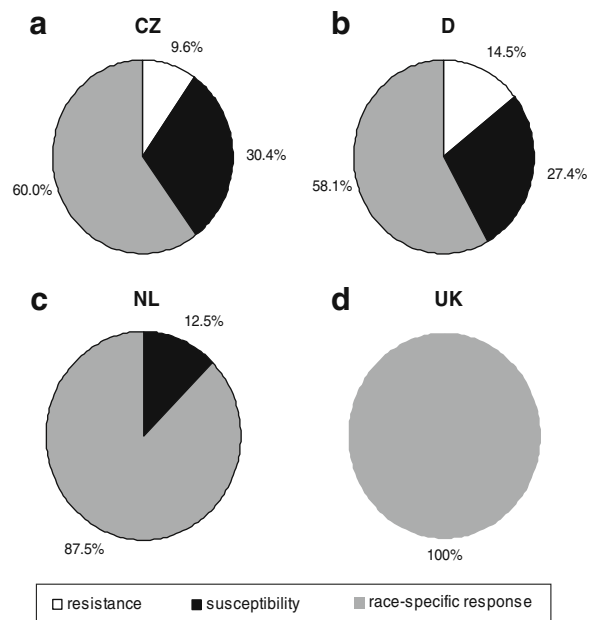


**Fig. 7** Distribution of resistance to *Bremia lactucae* among *Lactuca serriola* populations in four European countries (adapted according to data published in Lebeda et al. 2008). Figure shows a proportion of local populations of *L. serriola* with a high level of resistance, susceptibility, race-specificity and intra-population variation in race-specificity to the used set of *B. lactucae* races in each of the studied European populations (a–d)

individuals (Figs. 8c, d) are similar to those of the entire NL and UK populations.

#### *Spatial distribution of race-specific resistance to B. lactucae across Europe*

Of particular interest is the geographic distribution of race-specific resistance to *B. lactucae* within Europe. The spatial arrangement of local host populations showing resistant, susceptible and race-specific responses is depicted in Fig. 9. Within the Czech Republic, resistant populations of *L. serriola* were mainly located in the western parts. One resistant population was also found in the eastern part of the Czech Republic; however, susceptible populations (or those with mixtures of highly resistant and susceptible individuals) were more frequently found there. German populations of *L. serriola* were examined on two transects across the country (Fig. 1). Populations of



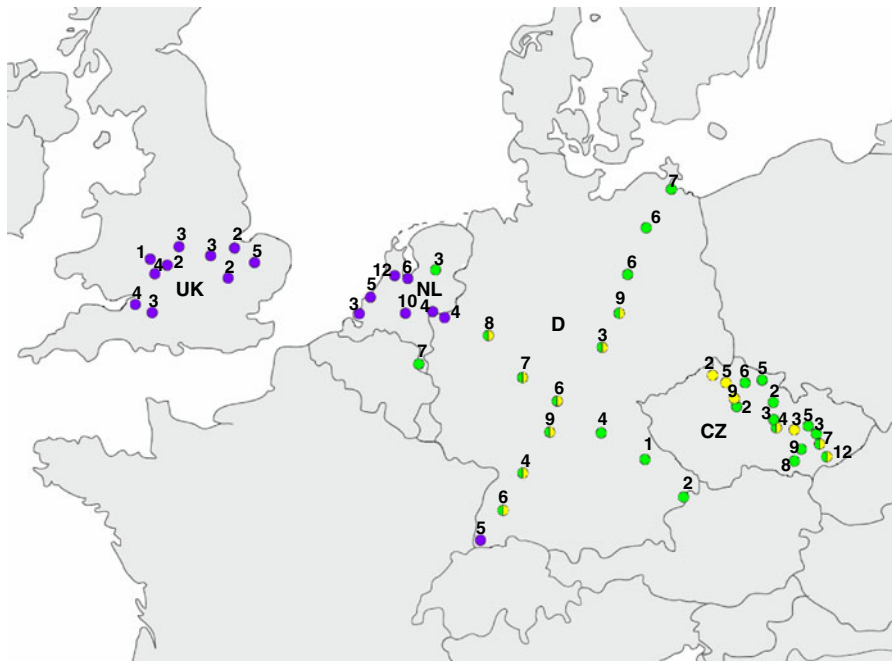
**Fig. 8** Distribution of resistance to *Bremia lactucae* among *Lactuca serriola* individuals ( $n=752$ ) in four European countries. Figure shows a proportion of *L. serriola* individuals which were completely resistant, completely susceptible or expressed race-specific response to the used set of *B. lactucae* races in each of the studied European populations (a–d)

*L. serriola* in the middle parts of Germany showed strong intra-population variation in their resistance to *B. lactucae*; while in the marginal parts of transects in eastern parts of Germany susceptible populations prevailed. Close to the border with the Netherlands one population with more pronounced race-specificity was found; another one was located in the south-western part of the country. As already mentioned, most Dutch populations displayed clear race-specificity. However, two highly susceptible populations were found in the border area near Germany. Interestingly, in the United Kingdom only populations with clear race-specific response were recorded (Fig. 9).

#### *Analysis of within-population variation in resistance to B. lactucae*

##### *Variation in complexity of resistance of the local L. serriola populations to the used set of B. lactucae races*

The other aim of our research was to determine the intra-population variation in resistance to *B. lactucae*,



**Fig. 9** Spatial distribution of race-specific resistance of *L. serriola* to *Bremia lactucae* across the European area. *Yellow spots* represent local populations of *L. serriola* with a high level of resistance; *green spots* local populations of *L. serriola* with a high level of susceptibility. Numbers close to the spots express the total amount of R-phenotypes described within a local population (i.e. intra-population variation in race-specificity);

*violet spots* local populations with a high level of race-specificity (i.e. strong differential response to the used *B. lactucae* races); *green spots* local populations of *L. serriola* with a high level of susceptibility. Numbers close to the spots express the total amount of R-phenotypes described within a local population

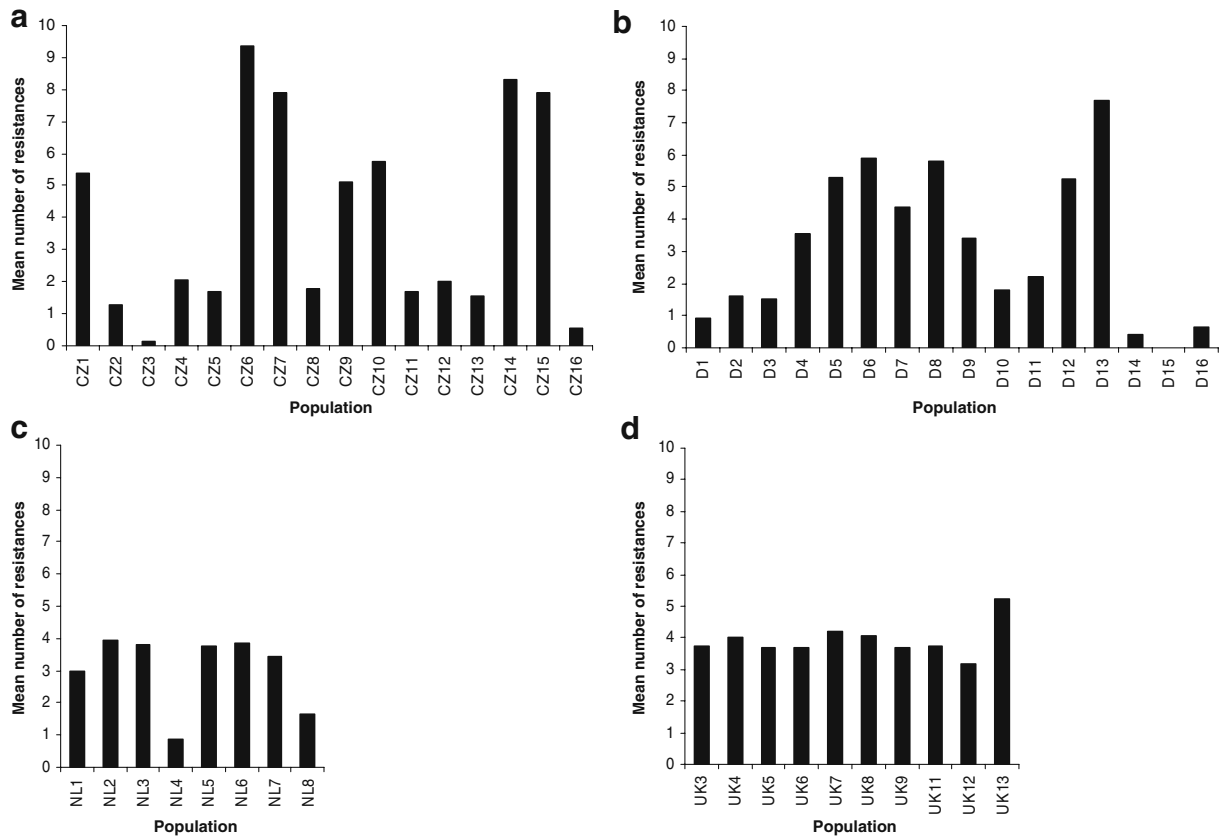
and to compare particular local populations of *L. serriola* in the European countries studied. First, we quantified the mean number of resistances of individuals within 50 local populations of *L. serriola*. As shown in Fig. 10, the highest mean resistance (>8) was found for populations CZ6, CZ7, CZ14, CZ15, and D13, (which means that all individuals in these populations had highly complex resistance patterns to the races of *B. lactucae*). However, none of these populations as a whole displayed complete resistance to all 10 races used. A medium level complexity of resistance (the mean resistance of individuals to 5–6 races) was recorded for some other CZ and D populations (e.g. CZ1, CZ9, CZ10, D5, D6, D8, and D12); mostly due to a more pronounced intra-population variation in the resistance of individuals. However, in the Czech Republic and Germany there were many local populations (CZ2–CZ5, CZ8, CZ11–CZ13, CZ16, D1–D3, D10, D11, D14–D16) which were almost or completely susceptible, and thus observed complexity of resistance was low (mean resistance of individuals to only 1 or 2 races). Two almost completely susceptible populations (NL4 and

NL8) were also found in the Netherlands. With that exception, all NL and UK local populations expressed medium levels of resistance complexity (typically mean resistance to 4 races; Fig. 10c, d).

To evaluate where to search for potential sources of new and efficient resistances we specified the overall resistance of individual local populations of *L. serriola* using the same criteria as shown in Figs. 4 and 7. Local populations were categorized according to the predominant responses of host individuals to 10 races of *B. lactucae* (Table 2). From the Table again it is evident that most of the resistance to *B. lactucae* recorded in the local populations of *L. serriola* studied was race-specific.

#### *Heterogeneity of the local populations of L. serriola*

Despite the highly uniform outward responses of many populations of *L. serriola* (resistant, susceptible, or race-specific) more or less pronounced intra-population variation in race-specificity was common in most local populations. Individuals with the same level of resistance complexity (either low or high) often



**Fig. 10** Relative complexity of resistance of the local populations of *Lactuca serriola* to the used set of *Bremia lactucae* races ( $n=10$ ). Complexity of resistance was expressed as a mean number of races against which resistance of examined individuals was

displayed within individual local populations of *L. serriola* in four European countries (**a–d**): 0=no resistance to used races of *B. lactucae*, 10=resistance to all used races

differed in the identity of those *B. lactucae* races to which they expressed resistance or susceptibility. Thus, local population resistance did not generally correlate with the total number of resistance (R-) phenotypes recognized. We expressed that discrepancy as heterogeneity or homogeneity of the local populations.

Figure 11 demonstrates that the degree of heterogeneity (proportion of individuals differing in their R-phenotype) varied broadly among the local populations, both within individual countries and within the entire European metapopulation. The D, NL and some CZ populations were among the most heterogeneous, while UK populations were the most homogeneous. The only exception to this was UK13; in this case the result is largely distorted by the small sample size (only 4 individuals examined). However, highly homogeneous local populations were also found in the Czech Republic (e.g. CZ1-CZ4, CZ6-CZ8, CZ13, CZ14, and CZ16),

Germany (D5, D8, D14–D16), and the Netherlands (NL2, NL4, and NL5).

Phenotypic characterization of *L. serriola* individuals

#### *Diversity of L. serriola* resistance phenotypes in four European countries

R-phenotypes were described on the basis of reaction patterns of *L. serriola* seedlings derived from seed collections (as described above) to the set of *B. lactucae* races. On the whole, 89 different R-phenotypes were recorded in the studied European metapopulation, among the set of 752 *L. serriola* samples included in our study (Table 3). Regardless of the unequal numbers and sample sizes of the studied European populations, it is evident that there were differences in the diversity of R-phenotypes among countries with the highest



**Table 2** Characterization of individual local populations of *Lactuca serriola* for resistance to *Bremia lactucae*

Response <sup>a</sup>	Local populations
High level of resistance <sup>b</sup>	CZ6, CZ7, CZ14, CZ15
High level of susceptibility <sup>c</sup>	CZ2, CZ3, CZ4, CZ5, CZ8, CZ11, CZ12, CZ13, CZ16, D1, D2, D3, D14, D15, D16, NL4, NL8
High level of race-specific response <sup>d</sup>	D10, D11, NL1, NL2, NL3, NL5, NL6 <sup>f</sup> , NL7, UK3, UK4, UK5, UK6, UK7, UK8, UK9, UK11, UK12, UK13
Intra-population variation in race-specificity <sup>e</sup>	CZ1, CZ9 <sup>f</sup> , CZ10 <sup>f</sup> , D4, D5 <sup>f</sup> , D6, D7 <sup>f</sup> , D8, D9 <sup>d</sup> , D12 <sup>d</sup> , D13 <sup>f</sup>

<sup>a</sup> Categorization same as in Figs. 4 and 7

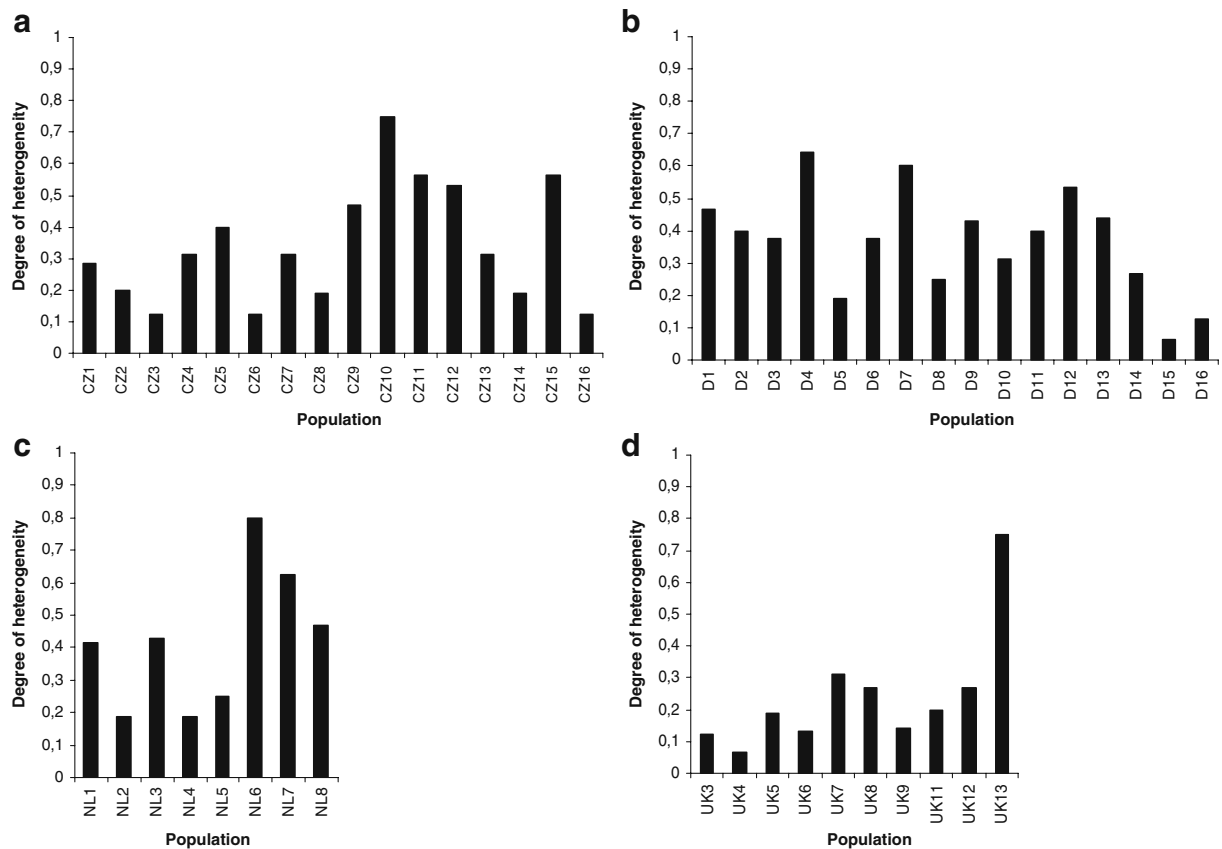
<sup>b</sup> Population composed of individuals with highly complex race-specific resistance patterns

<sup>c</sup> Population composed of individuals with lowly complex race-specific resistance patterns

<sup>d</sup> Whole populations or their big parts expressing high uniformity in their resistance resp. susceptibility to several races of *B. lactucae* (i.e. strong differential response to used races)

<sup>e</sup> Mixture of individuals with various race-specific reaction patterns characterized with high level of resistance and susceptibility occurring within one population

<sup>f</sup> Occurrence of individuals with intermediate susceptibility, i.e. reduced sporulation of a pathogen (ca 30–50%) on most plants included in a resistance test



**Fig. 11** Heterogeneity of the local populations of *Lactuca serriola* in four European countries (**a-d**). The degree of heterogeneity is expressed as a ratio between a total number

of tested individuals in the local populations and a number of recognized resistance phenotypes:  $>0$ =high homogeneity of a local population,  $\leq 1$  = high heterogeneity of a local population

**Table 3** Diversity of resistance phenotypes of *Lactuca serriola* recognized in four European countries and within the entire European metapopulation

Population (n=number of samples)	Total number of recognized R-phenotypes <sup>a</sup>	Number of the most frequent R-phenotypes (% of samples)
CZ (n=250)	45	8 (78.8)
D (n=241)	34	7 (77.6)
NL (n=120)	27	5 (64.2)
UK (n=141)	10	2 (84.4)
European metapopulation (n=752)	89	14 (82.3)

<sup>a</sup> different reaction patterns of individual *L. serriola* samples are described as R-phenotypes (or resistance phenotypes) characterized by specific combinations of resistant (-) and susceptible (+) reactions to the used *B. lactucae* races (n=10)

relative diversity (in proportion to sample size) being recorded in the Netherlands (a total of 27 R-phenotypes). High numbers of *L. serriola* R-phenotypes were also recognized in the Czech Republic and Germany (a total of 45 and 34 phenotypes respectively). However, individual R-phenotypes were unevenly distributed among the local populations, both within and among the four countries studied; additionally, their prevalence were generally relatively low.

The lowest diversity of R-phenotypes was recorded in the United Kingdom. A total of 10 R-phenotypes were recognized, with only two prevalent among 84.4% of all of the UK samples tested (Table 3).

#### *Resistance patterns and prevalence of recognized L. serriola resistance phenotypes*

A list of the major R-phenotypes, with their prevalence across the entire European metapopulation of *L. serriola*, as well as within individual countries is given in Table 4. The most commonly distributed R-phenotype (20.9% of all samples) was susceptible to all ten races of *B. lactucae*, and it was recorded in all countries studied with the exception of the UK. It was the most dominant R-phenotype in CZ (distributed in 12 out of 16 populations, and represented by 30.4% of the CZ individuals) and D populations (in 14 out of 16 populations, with a prevalence of 27.4% of the D individuals). The second most frequent R-phenotype was resistant to pathogen lines Bl:1, Bl:5, Bl:15, and

Bl:17 (18.1% of the samples tested), and was mostly distributed in the NL and UK populations, where it was the most prevalent R-phenotype. The third most frequent R-phenotype (7.8% of the samples) was resistant to all ten *B. lactucae* races and, as stated above, it was only present in some CZ and D populations.

When comparing the resistance patterns of R-phenotypes recognized in individual countries, large differences were found. Phenotypically, the CZ and D populations were very similar. They were characterized by four main groups of R-phenotypes (Table 4). As mentioned above, most frequent was the R-phenotype with susceptibility to all ten races of *B. lactucae*. A large number of CZ and D samples were described by high susceptibility to the majority of isolates used, with resistance only being expressed against Bl:12 and/or Bl:15, and/or Bl:17. The other most frequent R-phenotype was characterized by resistance to all ten isolates of *B. lactucae*. There also were quite a large number of highly resistant samples with susceptibility only to race Bl:21 and/or Bl:24. In the NL populations, the most frequent R-phenotypes were characterized by various combinations of resistance to Bl:1, Bl:5, Bl:12, Bl:15, and Bl:17, plus susceptibility to other races; however, the completely susceptible R-phenotype was also quite frequent. In the UK populations there were only two broadly distributed R-phenotypes (the first one with resistance only to Bl:1, Bl:5, Bl:15, and Bl:17; the second with resistance only to Bl:1, Bl:5, and Bl:15). Both of these were also recorded in the D and NL populations, but there the frequency of occurrence was much lower (Table 4).

#### Discussion

This study is probably the first detailed research focused on host resistance variation in plant-oomycete interactions in a wild plant pathosystem. When studying host-pathogen interactions it is difficult to draw authoritative conclusions from results based only on studies of local populations. Spatial structure is a critically important factor for host-pathogen dynamics in nature, and the metapopulation framework has proven to be useful for investigating the ecological and evolutionary dynamics of spatially structured host-pathogen associations in nature (Thrall and Burdon 1997). Most papers dealing with population biology and the ecology of hosts (as well as their

**Table 4** Frequency and distribution of the most common resistance phenotypes in the European metapopulation of *Lactuca serriola*

Race of <i>B. lactucae</i> /resistance phenotype of <i>L. serriola</i> <sup>a</sup>										Total number of samples (%)	Number of samples/populations			
Bl:1	Bl:5	Bl:12	Bl:14	Bl:15	Bl:16	Bl:17	Bl:18	Bl:21	Bl:24		CZ	D	NL	UK
+	+	+	+	+	+	+	+	+	+	157 (20.9)	76/12	66/14	15/3	0/0
–	–	+	+	–	+	–	+	+	+	136 (18.1)	0/0	10/2	37/5	89/9
–	–	–	–	–	–	–	–	–	–	59 (7.8)	24/5	35/9	0/0	0/0
+	+	+	+	–	+	+	+	+	+	45 (6.0)	14/5	26/7	5/4	0/0
–	–	–	–	–	–	–	–	+	+	45 (6.0)	28/6	17/6	0/0	0/0
–	–	+	+	–	+	+	+	+	+	39 (5.2)	0/0	2/2	7/3	30/8
+	+	–	+	+	+	+	+	+	+	34 (4.5)	19/3	15/4	0/0	0/0
+	+	+	+	+	+	–	+	+	+	23(3.0)	11/4	3/2	9/1	0/0
+	+	–	+	–	+	+	+	+	+	22 (2.9)	1/1	18/7	3/1	0/0
–	–	–	–	–	–	–	–	+	–	17 (2.3)	17/4	0/0	0/0	0/0
–	–	–	+	–	+	–	+	+	+	14 (1.9)	0/0	0/0	9/6	5/3
–	–	–	–	–	–	–	–	–	+	9 (1.2)	8/4	1/1	0/0	0/0
+	+	+	+	–	+	–	+	+	+	8 (1.0)	6/3	1/1	1/1	0/0
–	–	+	–	–	+	–	+	+	+	8 (1.1)	0/0	0/0	0/0	8/3
Other (altogether 75 different host R-phenotypes, each represented by less than 8 samples)										136 (18.1)	46/11	47/12	34/4	9/4
Totally										752 (100)	250/16	241/16	120/8	141/10

<sup>a</sup>Symbols used in the table

+ susceptible response

– resistant response

pathogens) in wild pathosystems have shown that in a highly fragmented landscape the best approach to the study of population structure and its variation is to consider populations as semi-independent units which are inter-connected to varying degrees by migration and gene flow (Thrall et al. 2001). There may be regional differences in local selection pressures, exerted by species interacting with one another, and influenced by environmental factors, which result in variation among local populations within a metapopulation (Laine 2005). Gene flow causes changes in gene frequencies through the reduction of differentiation among populations, and an increase of within-population variation by the mixing of individuals from populations subjected to different selection pressures (Papa and Gepts 2004). Thus, patterns of local adaptation are intensely affected by dynamics and migration rates of both host and pathogen, as well as the scale of the gene flow (Gandon et al. 1996; Thrall and Burdon 1997; Laine 2005).

The metapopulation concept is of particular relevance to host plant-obligate parasite interactions where the pathogen lacks free-living stages. In such

systems, where pathogen persistence is tightly linked to its host, the effect of fragmentation and the degree of population isolation may be exacerbated (Burdon et al. 2006). This is especially true in pathosystems, such as *Lactuca* spp.-*B. lactucae*, which adhere to the principles of the gene-for-gene theory (Lebeda et al. 2001b, 2002; Kuang et al. 2008). In this paper we only focused on the resistance structure of the host. Within the framework of the EU “Gene Mine” project the main task of our working group was to compare the spatial structure of resistance to *B. lactucae* in different parts of the European *L. serriola* metapopulation (Lebeda et al. 2007a) following an east-to-west transect of distribution including four countries (Czech Republic, Germany, Netherlands, and United Kingdom). The aim was to quantify variation in resistance within the entire European *L. serriola* metapopulation and its distribution among the four main regions, as well as among individual local populations (Lebeda et al. 2007a). At the same time, we searched for possible novel sources of resistance for lettuce breeding (Lebeda et al. 2007a, b, 2009a).



In general, the European metapopulation of *L. serriola* showed limited resistance to the races of *B. lactucae* used in the inoculation studies (Fig. 4); however broad variation in the complexity of resistance patterns was found at both population (Fig. 6) and individual (Fig. 10) levels. In total, 34% of the populations examined and about 21% of the samples tested displayed high susceptibility. On the other hand, completely resistant individuals only represented 7.8% of the samples of *L. serriola* tested; these were only found in CZ and D populations. In addition, there was considerable within and among-population diversity with regard to recorded R-phenotypes (Table 2). Our results showed that *L. serriola* plants with completely different R-phenotypes may grow in close proximity, within the local population. Similar patterns have also been observed in other wild pathosystems like *Linum marginale-Melampsora lini* (Burdon and Thompson 1995) or *Senecio vulgaris-Erysiphe fischeri* (Bevan et al. 1993b). Conversely, we observed the same phenomenon (i.e. variation in virulence at very fine spatial scales) within local populations of the pathogen, *B. lactucae* (Lebeda and Petrželová 2004a).

Because of the broad variation in resistance of *L. serriola* recorded within Europe, we were curious to know how resistance to *B. lactucae* was distributed across the transect area. The resistance data indicate that race-specific resistance is the most common type of resistance in the European *L. serriola* metapopulation, but resistance to some races is unequally distributed among individual geographical regions. Further, there were clear geographical differences in the genetic diversity of the resistance in individual areas. These results confirm the importance of viewing population studies over larger geographic areas in the metapopulation context (Thrall and Burdon 2002).

The Czech populations were the most variable of all those evaluated. They expressed high variability in their responses to individual races of *B. lactucae*. A large part of the CZ populations were highly susceptible to the races of *B. lactucae*; however, on the other hand, the Czech Republic was the only geographic region within the distribution of *L. serriola* where local populations with high levels of resistance were found (Lebeda et al. 2008). Within some of the CZ populations, high intra-population variation in resistance to the isolates of *B. lactucae* was recorded. At the level of individuals, high variation was found in both

the structure (Table 4) and complexity (Fig. 10) of the recognized resistance phenotypes; and numerous individuals were characterized by race-specific responses.

With regard to interactions between *L. serriola* and *B. lactucae* in the Czech region, we have extensive knowledge of pathogen virulence patterns, as well as of their spatial and temporal variation, obtained during long-term research on this system (Lebeda et al. 2008; Lebeda and Petrželová 2004a; Petrželová and Lebeda 2004b). This provides an opportunity to compare spatially-structured patterns of host resistance and pathogen virulence. For example, over multiple years in the Czech population of *B. lactucae* there were one or a few v-phenotypes prevalent in the pathogen population, and a broad range of other phenotypes that were much less abundant, with number and identity of the prevalent ones varying among years (Lebeda et al. 2008). For the Czech population of *L. serriola* we only have comprehensive data for 2001, but it is evident that the basic patterns of the population structure are similar to that of *B. lactucae*. Eight R-phenotypes were plentiful in CZ populations, representing 78.8% of the individuals examined (the total number of recognized R-phenotypes in the Czech Republic is 45). Similar population structures (i.e. high heterogeneity among host populations and dominance by a few R-phenotypes) have been found in the *Senecio vulgaris-Erysiphe fischeri* (Bevan et al. 1993b; Clarke and Akhka 2002) and *Linum marginale-Melampsora lini* interactions (Burdon and Thrall 2000; Thrall et al. 2001). Theory suggests that in nature, the persistence of polymorphisms in host-pathogen associations are likely to be maintained by continual cycles of coevolution within local populations, combined with occasional immigration of new resistance and virulence genes (Frank 1992; Barrett et al. 2008).

Because we currently lack data on the temporal and spatial dynamics of resistance in populations of *L. serriola* over time we cannot assess the extent to which changes over time and space in host resistance are linked to shifts in pathogen virulence. However, several papers dealing with other wild pathosystems, e.g. *Linum marginale-Melampsora lini* (Burdon and Thrall 2000; Thrall and Burdon 2002) or *Microbotryum* (= *Ustilago*) *violaceum* (Delmotte et al. 1999), have shown that the within- and among-population spatial structure and dynamics are principally different for host and pathogen populations. For example in the *L. marginale-M. lini* interaction,

within-population variation and diversity is much greater for host plants than for the pathogen (Thrall et al. 2001). Spatial models of gene-for-gene interactions suggest that this may be a general pattern (Thrall and Burdon 2002). At the among-population level, high overall differentiation has been recorded for both species in interactions between *M. violaceum* and its host plants, but it was much greater for the pathogen, which may indicate gene flow is lower among pathogen populations relative to the host (Delmotte et al. 1999).

The resistance structure of German and Czech populations of *L. serriola* was similar with regard to the number of highly susceptible individuals, but in Germany there were a much larger number of populations that had shown within-population differentiation in the resistance of individuals. In the German populations, high diversity of R-phenotypes was found and the identities of most dominant ones were the same as in the Czech Republic. Unlike in the Czech Republic, completely resistant individuals were widely distributed among populations. Interestingly, when looking at the distribution of resistance across Europe, one can see that resistant Czech populations are mainly located in the western part of the country. Westwards, towards central Germany, there are populations containing mixtures of susceptible and resistant individuals, while most of the other German populations are composed of only highly susceptible individuals. One study says that in pathogen metapopulations, where local populations are at least partially isolated but connected by gene flow, those populations are likely to contain genotypes that have coevolved locally with host populations as well as recently arrived genotypes from other host populations (Laine 2005). Similarly, for distribution patterns of resistant and susceptible individuals recorded within German populations of *L. serriola*, we hypothesize that resistant individuals may represent migrants from the resistant Czech populations to an area with otherwise susceptible populations.

There was a radical change in *L. serriola* resistance structure in the Netherlands. Here, most host individuals exhibited clear race-specific responses (i.e. medium complexity R-phenotypes). However, we found an overlap between German and Dutch populations of *L. serriola*. One local population, with clearly pronounced race-specificity, was found in Germany near to the Netherlands border; conversely, two local populations with high susceptibility were found in the

Netherlands close to the border with Germany. As for the phenotypic composition, relatively high variation at the level of R-phenotypes was found in the Netherlands. Some overlap between adjacent German and Dutch populations was also found in the occurrence of particular R-phenotypes (data not shown).

In the United Kingdom all populations were characterized by clear race-specific responses (Fig. 8) which agreed with previously reported results (Crute 1987). Interestingly, the diversity of R-phenotypes in the UK populations was quite low, with two types representing 84% of all UK individuals (Table 4). In addition, there were several other R-phenotypes with clear race-specificity, which were unique to the UK populations. Despite the overall low diversity, the phenotypic composition was very similar to that of the NL as UK populations shared the most dominant R-phenotypes with the NL populations. Thrall et al. (2001) also observed that populations of *Linum marginale* growing close together were more similar in phenotypic patterns of resistance to *Melampsora lini* isolates.

To summarize, large within- and among-population diversity of R-phenotypes of *L. serriola* recorded in this study was approximately evenly distributed across continental Europe (Fig. 9). In contrast, overall within- and among-population diversity of R-phenotypes was extremely low in the United Kingdom. However, there was a clear gradient of increasing race-specificity of *L. serriola* populations moving from central Europe towards the Atlantic coast, as seen in a preliminary analysis (Lebeda et al. 2008). There was a shift to balanced resistance towards western Europe, which was expressed in different ways among the studied regions. Within the Czech Republic we observed a mosaic of resistant, mixed and susceptible populations of *L. serriola*, although the latter prevailed. Towards the west, a more pronounced balance between resistant and susceptible individuals was recorded at the within-population level. In the Netherlands *L. serriola* individuals did not differ much in resistance levels (i.e. complexity), but they expressed a balance between resistance and susceptibility to a spectrum of pathogen races at the level of their phenotypes, which was described as a strong race-specific response. Populations were most balanced in the United Kingdom, where two R-phenotypes providing resistances to particular combinations of pathogen races were almost only distributed across the whole area studied; i.e. individuals did not differ largely either in their

resistance complexity or in recognized reaction patterns in UK. Modern agriculture now frequently employs breeding strategies simulating the more diverse situations represented in nature to increase the effectiveness of crop plant resistance to diseases. Commonly used breeding approaches such as cultivar mixtures or gene pyramiding (Mundt 2002; Mundt et al. 2002; Pink 2002) may be considered as such an analogy to spatial structuring of resistance recently found in real natural populations of *L. serriola* across Europe. From our recent results it seems that, at least under natural conditions, combination of both strategies (i.e. mixture of different plant genotypes and combination of resistance to various pathogen races within individual genotypes) is the most efficient, and provides the highest overall degree of resistance at the population level, which was most pronounced in NL and UK populations.

Kuang et al. (2008) reported a shift towards lower R-gene diversity of *L. serriola* moving westwards from the center of its origin and genetic diversity (presumed to be situated in the eastern Mediterranean). They supposed that during dispersion of this species to Europe it may have lost a large part of the original populations' genetic diversity. Recently, D'Andrea et al. (2006) studied genetic diversity of a wide range of *L. serriola* populations from western and central Europe using chloroplast (PCR-RFLP) and nuclear (microsatellites, SSR) markers. They revealed high genetic differentiation among individual populations. However, spatial pattern in gene diversity variation was significant only for populations isolated by greater distances. This is supported also by isozyme data (Dziechciarkova et al. 2004) and recent AFLP studies of European populations of *L. serriola* (Lebeda et al. 2009b). Further, D'Andrea et al. (2006) made a prediction map of the distribution of *L. serriola* gene diversity across Europe, which showed a decrease of diversity westwards and northwards from the areas with the highest values, which supports data published by Kuang et al. (2008). Among European areas with high gene diversities were eastern and central Europe, South of France and North of Italy, while lower gene diversities were recorded for populations from west Mediterranean (Portugal and Spain), South of Italy, United Kingdom, the Alps and Southern-Scandinavia (D'Andrea et al. 2006). Our resistance data correlate well with the predictions of D'Andrea (2006). Most CZ and D populations included in our resistance study are situated in regions with higher gene diversity,

which decreases towards the Netherlands and is the lowest in the United Kingdom.

Geographical-scale diversification of plant-pathogen systems has been shown in several other wild pathosystems, e.g. *Senecio vulgaris*-*Erysiphe fischeri* (Bevan et al. 1993b; Clarke and Akhka 2002), *Linum marginale*-*Melampsora lini* (Burdon and Thrall 2000), or *Plantago lanceolata*-*Podosphaera plantaginis* (Laine 2005). However, the first evidence for existence of a gradient of resistance in natural plant pathosystems was given by Springer (2007). He studied populations of California dwarf flax (*Hesperolinon californicum*) occurring along a south-north transect across California and observed a clear latitudinal cline in resistance structure to *M. lini*. Resistance levels were lowest in the north and increased gradually and continuously towards the south, and mirrored almost identically a cline in infection prevalence. For the wild *L. serriola*-*B. lactucae* pathosystem, we have no relevant data on pathogen occurrence across Europe except for the Czech Republic. Thus, we are not able to examine the extent to which geographic patterns of resistance correlate with disease prevalence in this interaction.

Significant role in shaping resistance structure of a host population play both the level of patchiness and connectivity of the host populations within the larger metapopulation (Carlsson-Granér and Thrall 2002). Theoretically, spatial differences in resistance of *L. serriola* populations may be based on a range of factors. In gene-for-gene interactions, the spatial structure of populations may result from the availability of compatible host-pathogen pairs within the spatial mosaic of individuals, at any specific location and time. Furthermore, ephemerality of this annual weed host, ecological circumstances of local host populations, as well as agronomic management and weed control practices that may vary among countries, may indirectly participate in shaping the spatial structure of populations by influencing survivorship of specific R-genotypes in the landscape, regardless of their resistance or susceptibility. Possibly, unequal distribution of the two morphological forms (*L. serriola* f. *serriola* and *L. serriola* f. *integrifolia*) within the European metapopulation of *L. serriola* (Lebeda et al. 2001a, 2007a) may also contribute to observed differences in spatial distribution of resistance among the studied regions (Lebeda et al. 2008).

*L. serriola*, which is native to Mediterranean area, has undergone a large expansion over the past



250 years and has colonized most of Europe (D'Andrea et al. 2009). The main factors responsible for such a large spread of *L. serriola* into the new regions are especially global climate warming, increasing anthropogenic disturbance and ruderalization of environment, and development of transport networks (Hooftman et al. 2006; D'Andrea et al. 2009). The result is greater availability and better connectivity of disturbed and ruderal habitats, which may be colonized by *L. serriola* (D'Andrea et al. 2009). This is probably true for continental Europe. Our studies, focused on the ecogeography of *L. serriola* (Doležalová et al. 2001; Lebeda et al. 2001a, 2004, 2007a), show that in most European countries the highest densities of *L. serriola* populations were along transport corridors. However, when comparing the four countries included in this study, *L. serriola* occupied the broadest range of different habitats in the Czech Republic and there is an apparent decrease in the range of habitats of *L. serriola* towards the western parts of Europe (Lebeda et al. 2001a, 2007a). We hypothesize, therefore, that the level of connectedness of individual populations also decreases, which may in turn greatly influence the extent of among-population differences in resistance patterns.

In contrast, increasing isolation leads to lower frequency of population mixing and higher uniformity of populations, which may explain the situation in United Kingdom. We hypothesize that isolation from continental Europe by sea was of crucial importance in shaping the resistance structure of the UK *L. serriola* population (Lebeda et al. 2008, 2009b), with two possible explanations of the origin of such specific spatial structure. It may either result from extremely strong adaptation to the local pathogen populations, or it may originate from several founder events from the continental Europe (mainland to island migration). However, we may only speculate on this, as for the United Kingdom no data are available on the natural distribution of *B. lactucae* on weedy growing plants of *L. serriola* (Crute 1987; Lebeda et al. 2007a).

Of course, results on distribution and variation of resistance in European metapopulation of *L. serriola* may be largely influenced by the spectrum of *B. lactucae* races used for our resistance screening. However, the data summarized in this paper clearly showed that host-pathogen interaction in the wild plant pathosystem *L. serriola*-*B. lactucae* is predominantly

based on race-specificity. Patterns of race-specificity in host populations of *L. serriola* were geographically structured with decreasing diversity from continental (central) Europe to the Atlantic coast (UK). Host populations in central Europe (Czech Republic, Germany) were the most heterogeneous with regard to resistance diversity in clear contrast to the relatively homogeneous UK populations. These results support our previous suggestion that this pathosystem is suitable as a model system for the research of host-pathogen interactions in natural plant communities (Lebeda et al. 2008), as well as for further exploitation of resistance variation in lettuce breeding (Lebeda 1998; Lebeda et al. 2002; Lebeda and Zinkernagel 2003; Beharav et al. 2006; Lebeda et al. 2007b, 2009a).

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