Incidence of Lettuce Downy Mildew (*Bremia lactucae*) and Powdery Mildew (*Golovinomyces cichoracearum*) in Natural Populations of Prickly Lettuce (*Lactuca serriola*)

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Abstract

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The study was focused on the wild pathosystem *Lactuca serriola*–lettuce downy mildew (*Bremia lactucae*) and lettuce powdery mildew (*Golovinomyces cichoracearum*). Observations were focused mainly on recording natural infection of prickly lettuce (*Lactuca serriola*) by downy and powdery mildews in the East Bohemia and Moravia (the Czech Republic) in the May–September period of 2007–2011, and on the influence of environmental conditions on disease incidence. Only data for July and August were used for the detailed comparisons of occurrence of both pathogens, because intensity of disease in this period was the highest. Data were linked with the average monthly temperature and rainfall rate in the Czech Republic. *G. cichoracearum* prefers rather low levels of precipitation and temperatures around 20°C, therefore significantly higher incidence of this pathogen was recorded in August 2007. On the other hand in July 2009 and 2010, when the intensities of precipitation were higher, incidence of *Bremia lactucae* prevailed. In August 2010 and 2011 incidence of both pathogens were more or less similar at all locations. Our observations showed that climatic conditions influence the incidence and prevalence of both pathogens in weedy growing populations of *Lactuca serriola*.

Keywords: wild plant pathosystem; disease incidence; disease prevalence; temporal changes; co-incidence of pathogens; climatic conditions

Abbreviations: BL – *Bremia lactucae;* GC – *Golovinomyces cichoracearum*

Wild plant pathosystems involve a wild plant, the pathogen that attacks and feeds on it, and the environment that affects both the plant and the pathogen. Despite the common occurrence of plant pathogens in natural systems, it is still the case that more attention is paid to crop pathosystems. In the 1980s the first studies of wild plant pathosystems occurred (Burdon 1987; Burdon & Jarosz 1991). Since then a number of additional systems, mostly concentrated on biotrophic pathogens, have been studied (reviewed in Laine 2011).

There are several obvious differences between wild and crop plant pathosystems. The first is genetic diversity: in wild plant pathosystems both the host and the parasite populations exhibit great genetic diversity, while in crop pathosystems the host population normally exhibits high genetic uniformity and in the parasite population commonly low genetic diversity is assumed. Wild pathosystems may be therefore much more flexible in responses to environmental changes than crop pathosystems. The second difference lies in the fact that

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in wild plant pathosystems interactions between the parasites and their hosts are balanced which allows survival of both, while in crop pathosystems boom and bust cycles corresponding with vigorous epidemics are common and devastating (Robinson 1987).

As for the powdery mildews, much attention has been paid to the interaction between *Senecio* spp. and *Erysiphe* (newly *Golovinomyces*) *fischeri* (Bevan *et al*. 1993a,b,c). Some brief information about incidence of powdery mildew in wild *Lactuca* spp. populations has been published (Lebeda *et al.* 2001, 2008; Mieslerová *et al.* 2007). As for the downy mildews, one of the most intensively studied wild pathosystems is *Lactuca serriola–Bremia lactucae*. A close relationship was found between lettuce downy mildew severity and prevalence, and the type of habitat or size and density of *L. serriola* populations (e.g. Petrželová & Lebeda 2004a; Lebeda *et al.* 2008).

Prickly lettuce (*Lactuca serriola* L., family Asteraceae, subfamily Cichorioideae) is a plant species with preference for dry climatic conditions, mainly in mild and warm areas of the North Hemisphere. It occurs in Europe, Asia, Africa, Indonesia, and North and Central America (Lebeda *et al.* 2004). From an ecological point of view, prickly lettuce can be considered as r-strategist, given that it is an invasive pioneer plant species which readily colonises new habitats. *L. serriola* is part of the primary gene-pool of the genus *Lactuca* L. It is closely related to cultivated lettuce and is considered as its ancestor (de Vries 1997; Lebeda *et al.* 2007). Because of their large genetic diversity, plant progenitors like *L. serriola* are used for studies of resistance to diseases (Lebeda *et al*. 2008) and lettuce breeding (Lebeda *et al*. 2007).

The oomycete *Bremia lactucae* Regel causes one of the most devastating diseases of lettuce worldwide. This obligate pathogen is capable of infecting any lettuce growth stage from seedling to mature plant, and it sporulates mainly on the lower side of leaves. *B. lactucae* attacks not only the members of the *Lactuca* genus, but also more than 150 species and about 40 genera of the family Asteraceae (Crute & Davis 1977). In spite of its broad host range, individual isolates of *B. lactucae* are highly host-specific and mostly limited to the same host plant species or genus (Lebeda *et al.* 2002). In total, 17 wild species of the genus *Lactuca* are described in Europe. However, only 7 of them can be considered as natural hosts of *B. lactucae* (Lebeda *et al*. 2002). The most common wild host of this pathogen is *L. serriola* (Lebeda *et al.* 2008). The interaction between *L. serriola* and *B. lactucae* generally conforms to a gene-for-gene relationship (Crute 1992a), in which resistance of the hosts is determined by dominant *Dm* resistance genes (or R-factors) matched by dominant avirulence factors in the pathogens (Lebeda *et al.* 2008).

Golovinomyces cichoracearum sensu stricto (DC.) V.P. Gelyuta is a powdery mildew fungus belonging to *Ascomycetes*. It can be a serious pathogen of cultivated chicory and lettuce crops, especially in the USA (Lebeda 1985; Crute 1992b; Davis *et al.* 1997; Braun 1999). *G. cichoracearum s. str.* has a world-wide distribution and its host range includes more than 100 genera and about 500 species of the family Asteraceae (Lebeda & Mieslerová 2011). The disease is favoured by moderate to warm temperatures and relatively dry weather conditions. Interactions between wild *Lactuca* species and *G. cichoracearum s. str.* have been studied since 1985 (Lebeda 1985, 1994). A total 99 accessions of seven wild *Lactuca* species were tested for the natural infection of *G. cichoracearum* in a glasshouse. In general, *L. serriola* accessions were found to be highly susceptible (Lebeda 1994). To increase the possibility of more detailed studies of GC populations for a pathogenic variability and its temporal changes, a basic differential set of *Lactuca* spp. has been established (Lebeda *et al.* 2012). Later studies clearly demonstrated existence of race-specific interactions in the wild pathosystem *Lactuca* spp.–*G. cichoracearum s. str.* (Lebeda *et al.* 2013).

Several crop plants are known to suffer from serious infections by representatives of both main groups of biotrophic plant pathogens mentioned, i.e. powdery mildews (fungi) and downy mildews (oomycetes). Important examples are: cucurbits – *Podosphaera xanthii, Golovinomyces cichoracearum* (powdery mildews) and *Pseudoperonospora cubensis* (downy mildew); hop – *Podosphaera macularis* (powdery mildew) and *Pseudoperonospora humuli* (downy mildew); grapevine – *Erysiphe necator* (powdery mildew) and *Plasmopara viticola* (downy mildew), and others. Interactions in these crop pathosystems have been studied intensively (Dhiman *et al.* 1995; Oliva *et al.* 1999; Pethybridge *et al.* 2003).

The aim of this paper was to describe relationships between the host (*Lactuca serriola*) and its two pathogens under conditions of natural infection. This pathosystem seems very interesting not only from the viewpoint of understanding mechanisms of interactions between three participants (host–pathogen–pathogen) but also allowing deeper insight into the relationships within a natural plant pathosystem with emphasis on environmental factors, e.g. temperature and rainfall.

MATERIAL AND METHODS

Field surveys. Observations were focused mainly on recording the natural infection of weedy growing prickly lettuce (*Lactuca serriola*) by downy mildew (*Bremia lactucae*) and powdery mildew (*Golovinomyces cichoracearum*) in localities in East Bohemia and Moravia (the Czech Republic; Figure 1) in the May–September period of 2007–2011. In most localities, observations were repeated in successive years in order to determine the dynamics of incidence of both pathogens in host populations. Wherever possible, isolates of *B. lactucae* and *G. cichoracearum* were collected and used for subsequent studies of their pathogenic variability.

Recorded characteristics. Two parameters were used to assess the distribution of *B. lactucae* and *G. cichoracearum*. The first was disease incidence (DI) expressed as a percentage of surveyed sites and populations of *L. serriola* with recorded *B. lactucae* or *G. cichoracearum*. The second parameter was disease prevalence (DP) expressed as a proportion of diseased individuals within a population using a 0–3 scale (Lebeda 1994, 2002; Petrželová & Lebeda 2004a; Lebeda *et al.* 2008): 0 = no visible symptoms of *B. lactucae* or *G. cichoracearum* infection; 1 = low DP with either occurrence of chlorotic spots on infected leaves associated with sparse or no visible sporulation of *B. lactucae* or sporadic occurrence of sporulating pustules of *G. cichoracearum*; 2 = medium DP with either medium occurrence of chlorotic or necrotic leaf spots with sporulation of *B. lactucae* or pustules of *G. cichoracearum* covering up to 50% of leaves and plants; 3 = high DP with either the majority of leaves and plants almost completely covered by chlorotic or necrotic spots with profuse sporulation of *B. lactucae* or the majority of leaves and plants covered by sporulating mycelium of *G. cichoracearum*. Plants were semiquantitatively visually surveyed (haphazard).

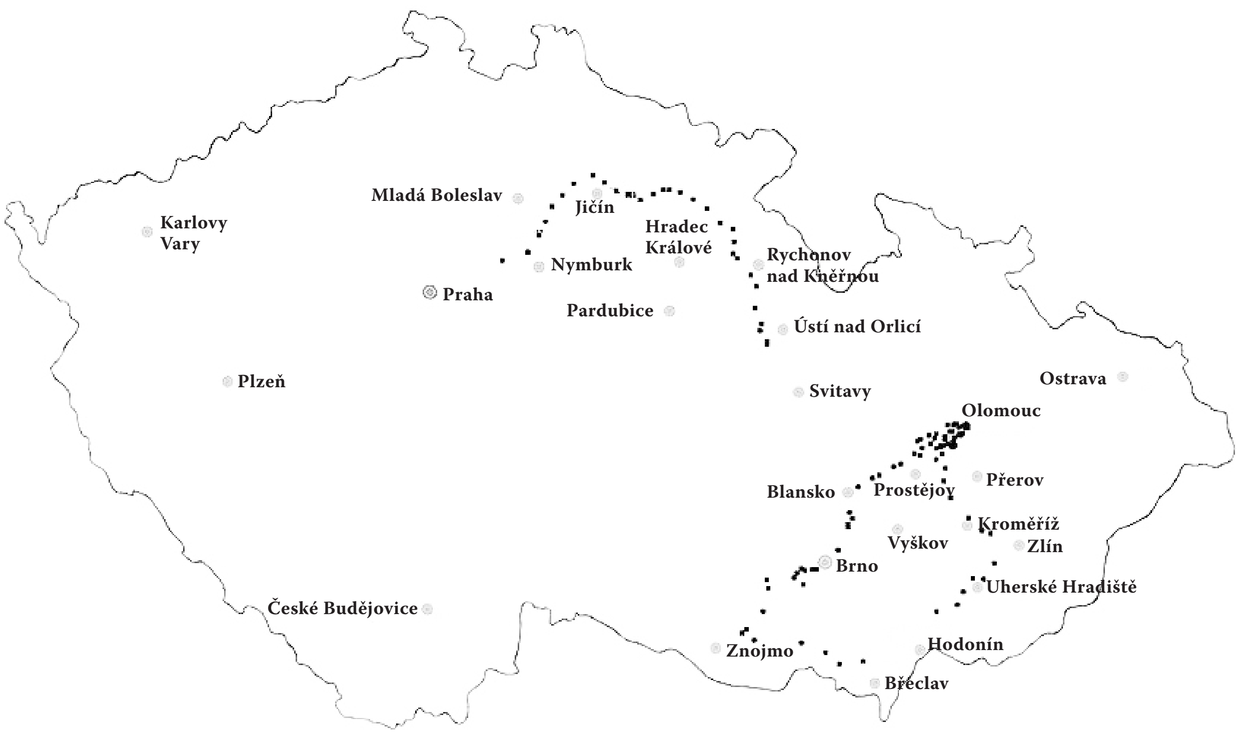

Figure 1. Localities (by dots) in the Czech Republic surveyed in the period 2007–2011 for occurrence of lettuce downy mildew (*Bremia lactucae*) and powdery mildew (*Golovinomyces cichoracearum*) in weedy growing *Lactuca serriola* populations

Table 1. Number of surveyed sites and populations of *Lactuca serriola* during 2007–2011

Sites in region	Number of observed				
	2007	2008	2009	2010	2011
Jihomoravský	22	26	21	21	21
Olomoucký	26	12	8	10	9
Zlínský	7	1	0	1	3
Moravskoslezský	2	0	0	0	0
Královéhradecký	13	18	15	20	11
Pardubický	6	9	10	10	8
Středočeský	8	12	13	10	6
Totally	84	78	67	72	58
Populations of *L. serriola*	108	90	73	102	66

Meteorological data. Recorded values of both incidence and prevalence of *B. lactucae* and *G. cichoracearum* in examined *L. serriola* populations fluctuated during the survey period 2007–2011, therefore we tried to compare records of disease occurrence with meteorological data, namely with the month mean temperatures and amounts of precipitation for the Czech Republic. Data were obtained from the following sources: http://www.chmi.cz/portal/dt?portal_lang=cs&menu=JSPTabContainer/P4_Historicka_data/P4_1_Pocasi/P4_1_4_Uzemni_teploty&last=false and http://www.chmi.cz/portal/dt?menu=JSPTabContainer/P4_Historicka_data/P4_1_Pocasi/P4_1_5_Uzemni_srazky.

RESULTS

Sites and populations of *L. serriola* examined for incidence of *B. lactucae* and *G. cichoracearum* during 2007–2011

Table 1 summarises the number of surveyed localities during the studied years. The best explored for the incidence of *B. lactucae* and *G. cichoracearum* were regions Olomoucký, Jihomoravský, and Královehradecký, followed by Středočeský, Pardubický, and Zlínský. The regions (Table 1) were chosen on the basis of our previous research (Lebeda *et al.* 2008). In those regions, there were well-studied sites with populations of *L. serriola*, and records were available on annual incidence of both pathogens.

Incidence of *B. lactucae* and *G. cichoracearum* in natural populations of *L. serriola*

Most populations of *L. serriola* were surveyed primarily in July and August, when the intensity of infections was the highest. In 2007 and 2008 the first symptoms of *B. lactucae* infection in populations of *L. serriola* were recorded in June (Table 2).

Table 2. Temporal incidence of *Bremia lactucae* (BL) and *Golovinomyces cichoracearum* (GC) in populations of *Lactuca serriola*

Year		Number of populations of *L. serriola* infected by a pathogen/total number of surveyed populations in months				
		May	June	July	August	September
2007	BL	–	3/3	11/15	34/88	0/2
	GC	–	1/3	9/15	64/88	2/2
2008	BL	0/1	31/44	22/40	1/5	–
	GC	1/1	21/44	20/40	5/5	–
2009	BL	0/7	–	44/66	–	–
	GC	4/7	–	27/66	–	–
2010	BL	–	–	36/68	21/34	–
	GC	–	–	11/68	24/34	–
2011	BL	–	–	15/24	22/42	–
	GC	–		9/24	20/42	–

– no data

Table 3. Monitoring of disease incidence and prevalence in natural populations of *Lactuca serriola* in 2007–2011

Year		Number of evaluated sites/ populations of *L. serriola*	Disease incidence (%)		Disease prevalence (%)		
			A	B	1	2	3
2007	BL	84/108	57.1	44.4	88.7	11.3	0
	GC		58.8	75.3	57.5	28.9	13.6
2008	BL	78/90	73.0	63.3	84.9	9.0	6.1
	GC		52.6	51.1	85.1	8.5	6.4
2009	BL	67/73	67.1	61.6	84.8	13.0	2.2
	GC		43.3	41.1	70.0	23.3	6.7
2010	BL	72/102	79.1	55.8	95.0	5.0	0
	GC		44.4	34.3	71.4	8.6	20.0
2011	BL	58/66	62.0	54.5	77.9	9.0	12.9
	GC		50.0	43.9	75.9	17.2	6.9

A – % of surveyed sites with *B. lactucae* (BL) or *G. cichoracearum* (GC); B – % of observed *L. serriola* populations with incidence of *B. lactucae* (BL) or *G. cichoracearum* (GC); 1, 2, 3 – % of observed *L. serriola* populations with different levels of disease prevalence (see Methods)

In the next years field surveys at those localities began in July so we were not able to record the start of infections. The last incidence of *B. lactucae* was recorded at the end of August and beginning of September (in 2007) when most *L. serriola* plants were already at the end of their life cycle. *G. cichoracearum* was first found in May 2008 and 2009, when no occurrence of *B. lactucae* was detected (Table 2). The last incidence of *G. cichoracearum* was recorded in September (in 2007).

During the period 2007–2011 the percentage of *L. serriola* populations infected (disease incidence) by *B. lactucae* varied between 44.4 and 63.3%, and by *G. cichoracearum* between 34.3 and 75.3% (Table 3). All infected populations of *L. serriola* were evaluated for disease prevalence. Infections by both pathogens were mostly light, although their prevalence in the studied populations fluctuated between years. The most common was DP = 1 (percentage of populations with DP = 1 ranged from 77.9% to 95% for *B. lactucae*, and from 57.5% to 85.1% for *G. cichoracearum*). The frequencies of populations with medium and high levels of DP were rather low, but their values were mostly higher

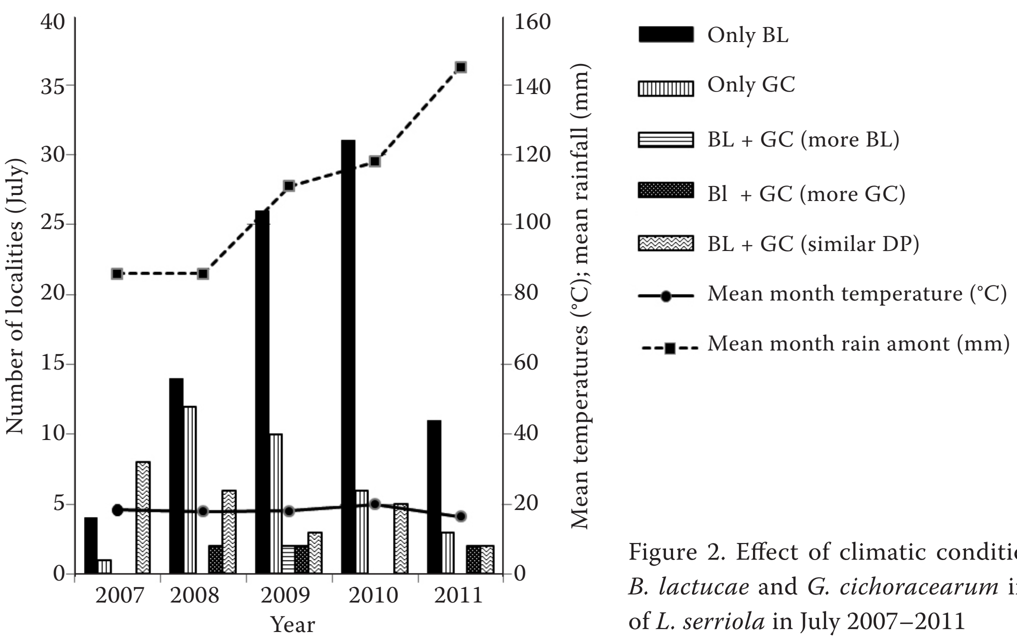

Figure 2. Effect of climatic conditions on occurrence of *B. lactucae* and *G. cichoracearum* in natural populations of *L. serriola* in July 2007–2011

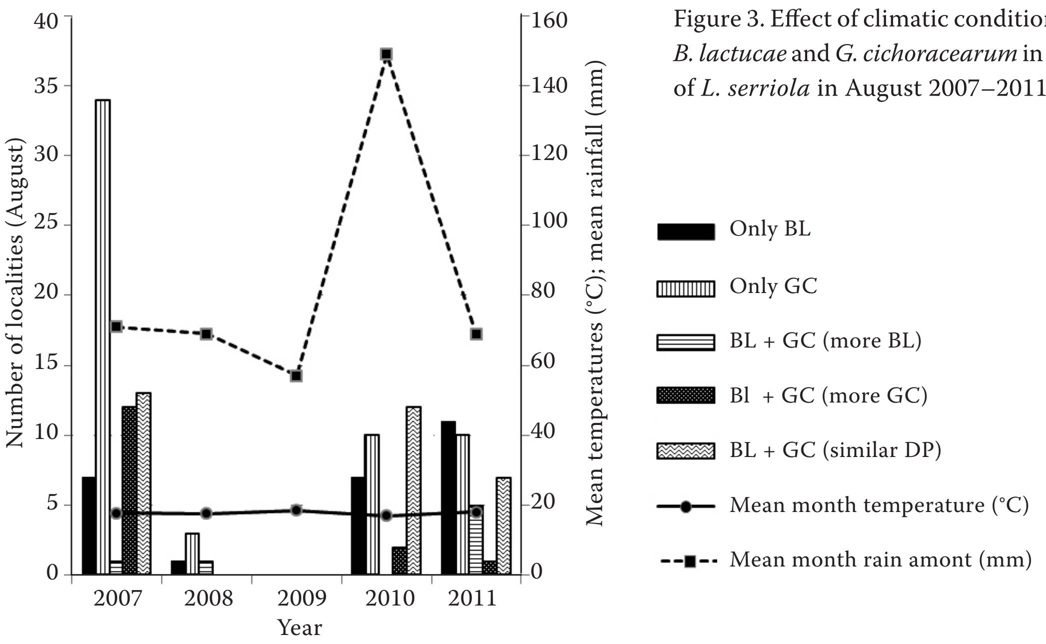

Figure 3. Effect of climatic conditions on occurrence of *B. lactucae* and *G. cichoracearum* in natural populations of *L. serriola* in August 2007–2011

for *G. cichoracearum* compared to *B. lactucae*. However *B. lactucae* occurred more frequently than *G. cichoracearum* in wild *L. serriola* populations in most years (Table 3).

Assessment of co-incidence of *B. lactucae* and *G. cichoracearum* in natural populations of *L. serriola* (2007–2011) and the effect of environmental conditions on this phenomenon

For detailed comparison of the co-occurrence of pathogens among individual years only data for July and August were used, when disease intensities of both pathogens were high. Unfortunately, the number of visited localities was not same in all years; data for August 2009 are missing. With respect to the incidence of both pathogens the localities with *L. serriola* populations were divided to 5 categories: A – localities with incidence of *B. lactucae* only, B – localities with incidence of *G. cichoracearum* only, C – localities with incidence of both pathogens with higher DP for *B. lactucae*, D – localities with incidence of both pathogens with higher DP for *G. cichoracearum*, E – localities with both pathogens with the same prevalence. Results are summarized in Figure 2. (for July) and Figure 3 (for August). The graphs show substantial fluctuations in the distribution of localities among these categories. However, in July populations of *L. serriola* infected only by *B. lactucae* prevailed during the whole period (2007–2011). Populations infected only by *G. cichoracearum* were also frequent, followed by populations with similar prevalences of both pathogens (Figure 2). In comparison, no similar pattern is apparent for data from August, the distribution of localities into the five categories is more balanced (Figure 3).

Epidemiological data in each category were linked with meteorological data, namely average month temperatures and month precipitation amount in the Czech Republic. Searching for correlations between the climatic conditions and incidence of *B. lactucae* and/or *G. cichoracearum* we can see that the rainfall rate in both months was very uneven during the studied period, while the mean temperatures did not fluctuate much (Figures 2 and 3). However, except for 2010 the mean monthly rainfall was significantly higher in July than August, which might explain the high frequency of populations with only *B. lactucae* that month. Those were the most frequent especially in July 2009 and 2010, when the average monthly rainfall was above normal (Figure 2). However, in August 2010 when rainfall was extremely high, the incidence of both pathogens was similar. Localities with only *G. cichoracearum* were the most frequent category in August 2007 and 2008 (Figure 3).

From the above observations-mentioned data it is obvious that the monthly precipitation (mainly in July) has a strong influence on the incidence of *B. lactucae* and *G. cichoracearum*, in accordance with their life histories. In contrast the temperature does not seem to have a significant effect on occurrence and representation of the studied pathogens in *L. serriola* populations, both in July and August (Figures 2 and 3).

DISCUSSION

Monitoring of lettuce downy and powdery mildew in natural populations of *L. serriola* revealed that incidence and prevalence of both diseases fluctuate during time. Our observations indicate that these fluctuations could be conditioned by variable climatic conditions. From our data it is evident that especially humidity could have a big influence on incidence of natural infections for the studied pathogens, as the temperatures did not vary distinctly during the evaluated months and years. Average monthly rainfall fluctuated significantly during the studied years. The long-time average amount of precipitations in July and August is 78–79 mm, however in some years the monthly average precipitations was much higher (in some cases nearly two times). The results from August 2007 and 2008 or from July 2009 and 2010 (Figures 2 and 3) show a clear relationship between environmental conditions and the occurrence of both pathogens, i.e. relatively dry months were preferred by *G. cichoracearum* and wet months by *B. lactucae*. Previously Mieslerová *et al.* (2007) recorded lower number of localities with incidence of only *B. lactucae* than only with *G. cichoracearum* in years with hot dry summers. Paradoxically, in August 2010 when rainfall for the month was extremely high, incidence of both *B. lactucae* and *G. cichoracearum* was more or less equal. Therefore, other factors must be considered to play a role in the infection and epidemiology of these two pathogens. Especially the host and pathogen genetic diversities could have a considerable importance.

Wildplant populations occur as mixtures of genotypes, so pathogen incidence is strongly dependent on the availability of susceptible host plants (Cousens & Croft 2000). Despite the fact that both *B. lactucae* and *G. cichoracearum* are characterised by a very broad host range, they were found to be highly host-specific (Lebeda *et al.* 2008; Staněk 2013). Collected isolates of both pathogens were mostly limited to the same host plant species or genus from which they were collected. The only exception is the confirmed ability of isolates of *B. lactucae* and *G. cichoracearum* from *L. serriola* to infect some *L. sativa* cultivars (Petrželová & Lebeda 2004a; Lebeda *et al.* 2012, 2013). Recent study of interactions of *L. serriola* genotypes with well characterised isolates of *B. lactucae* originating from *L. serriola* revealed low level of race-specific resistance of investigated *L. serriola* populations (Křenová 2013). Similar studies have not been done on *G. cichoracearum* isolates. Nevertheless, existence of a broad virulence variability has been shown for isolates of *B. lactucae* (Petrželová & Lebeda 2004a,b; Lebeda *et al.* 2008) and *G. cichoracearum* (Lebeda *et al.* 2013) originating from wild populations of *L. serriola*. Sexual reproduction and heterothallism could play an important role in genetic recombination of both *B. lactucae* and *G. cichoracearum* and are considered as major sources of virulence variation (Schnathorst 1959; Lebeda *et al*. 2008).

Optimal conditions for *G. cichoracearum* development are temperatures between 18 and 25°C (Schnathorst 1960a,b; Sogelová 2007) and drier climate (Schnathorst 1960b). *B. lactucae* prefers low temperatures for sporulation (10–15°C) and higher relative humidity (95–100%) (Su *et al.* 2004). Furthermore, *B. lactucae* also has specific demands for light (Crute & Dixon 1981; Nordskog *et al.* 2007). Despite having different environmental optima, *B. lactucae* and *G. cichoracearum* can occur together in wild *L. serriola* populations. However, with one exception (August 2007) *B. lactucae* was more frequent in wild populations of *L. serriola* although powdery mildew was found to be a generally more aggressive pathogen (Petrželová & Lebeda 2004a). Therefore, when both pathogens co-occurred, *B. lactucae* sparsely prevailed (Figures 2 and 3; Mieslerová *et al.* 2007). Schnathorst (1962) studied the relationships between downy and powdery mildew of lettuce occurring together in the Salinas Valley. He reported that these two diseases may occur alone or together and form three disease 'zones' in the valley. Differing macroclimatic conditions in these zones appeared to determine the presence and relative prevalence of both diseases. The author found that downy mildew is more abundant when the average temperature is low (13°C) and average humidity is high (88% RH), whereas powdery mildew is more abundant in areas with higher average temperatures (17–19°C) and lower average relative humidity (77% or less). He also reported mixed colony growth, i.e. powdery mildew grew over the portion of the leaf infected by downy mildew. We observed the same on leaves of *L. serriola* (unpublished results).

The wild pathosystem *L. serriola*–*B. lactucae* and *G. cichoracearum* is very complex and variable (Lebeda *et al*. 2008; Lebeda & Mieslerová

2011). Pathogen incidence was found to be strongly influenced by ecological factors, such as climatic and microclimatic conditions as well as by the host population (mainly by its genetic variability). Both studied pathogens infecting wild populations of *L. serriola* are shared also by crop (lettuce, *L. sativa*), which makes this wild pathosystem a good model for future research. Petrželová and Lebeda (2004a) postulated that the gene flow between crop and wild pathosystem *L. serriola–Bremia lactucae* is possible, which might increase variation in both pathogen and host population. In North America is for controlling of occurrence of lettuce downy mildew successfully used weather forecasting system (Wu *et al.* 2001)

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