

Distribution of Compatibility Types and Occurrence of Sexual Reproduction in Natural Populations of *Bremia lactucae* on Wild *Lactuca serriola* plants

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The occurrence of sexual compatibility types (mating types) was studied in a set of 59 *Bremia lactucae* isolates originating from 33 naturally infected and wild populations of *Lactuca serriola* (prickly lettuce) plants occurring in the Czech Republic, Germany and France. The isolates were collected in the period 1997–1999 as part of detailed population studies of virulence structure. Both compatibility types (B1 and B2) were recorded. However, the majority of the isolates was determined as type B2, with only two isolates being type B1. The reasons for and influence of this sexual structure are discussed in relation to the virulence of pathogen populations and interactions between wild and crop pathosystems. Occurrence of natural sexual reproduction of *B. lactucae* on *L. serriola* plants was extremely rare. Virulence variation of *B. lactucae* populations occurring on *L. serriola* would not seem to be related to sexual reproduction.

Keywords: Wild plant pathosystem, prickly lettuce, lettuce downy mildew, mating types, heterothallism, oospore formation.

Bremia lactucae Regel (lettuce downy mildew) is known as a highly variable pathogen (Lebeda and Schwinn, 1994) of cultivated lettuce (*Lactuca sativa* L.), some related wild *Lactuca* spp. and more than two hundred species of Compositae from about 40 genera of the tribes Lactuceae, Cynareae and Arctoideae (Crute and Dixon, 1981; Lebeda et al., 2002b). Recently at least 97 wild *Lactuca* spp., which mainly occur in Asia and Africa have been described, although species are found in Europe, and North and Central America (Lebeda and Astley, 1999; Lebeda et al., 2002a). However, detailed analysis of available data showed that *B. lactucae* infection on naturally growing plants has been recorded in only a limited number of *Lactuca* spp. (in total 14 species) and related genera which may be considered as natural hosts of this pathogen (Lebeda et al., 2002b). Some additional *Lactuca* spp. are known as potential hosts, but these data originate only from laboratory screening studies (Lebeda and Petrželová, 2001). In Europe, at least 16 wild growing *Lactuca* spp. (Doležalová et al., 2001; Lebeda et al., 2001) are described. *Lactuca serriola* L. (prickly lettuce) has a worldwide distribution and can be considered the commonest species of the genus in Europe where it is a widely distributed weed (Doležalová et al., 2001; Lebeda et al., 2001). *L. serriola* was found as the commonest natural

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Lactuca host species of *B. lactucae* (Lebeda, 1984; Lebeda and Syrovátka, 1988; Lebeda, 1998a; Petrželová and Lebeda, 2000; Lebeda et al., 2001; Lebeda and Petrželová, 2001; Lebeda, 2002). Race-specificity most frequently characterises interactions between wild *Lactuca* spp. and *B. lactucae* isolates (Lebeda et al., 2002b). However, their virulence variation and origin of this variation in wild-pathosystems is not well known until now (Lebeda, 1984, 1986; Lebeda and Blok, 1990; Lebeda and Boukema, 1991; Lebeda, 2002; Lebeda et al., 2002b).

Diverse sources participating in generating a considerable genetic variation of virulence in populations of plant pathogenic fungi have been described (Burdon, 1993; McDermott and McDonald, 1993; Burdon and Silk, 1997). Spontaneous point mutation, sexual recombination and somatic hybridization, with or without subsequent nuclear fusion and recombination, are the traditionally recognized mechanisms whereby variation is generated within individual pathogen populations (Burdon, 1993). In populations of *B. lactucae*, sexual reproduction has an important role in genetic recombination and is considered to be the major source of virulence variation (Crute, 1992; Lebeda and Schwinn, 1994; Lebeda and Zinkernagel, 2002).

B. lactucae is a peronosporaceous and evolutionarily advanced oomycete (Dick, 2000) with frequent occurrence of sexual reproduction. This process is characterized by formation of oospores, which are the thick-walled structures formed inside the host tissue and ensuring long-term survival of the fungus in unfavourable conditions. The course of *B. lactucae* oospore ontogenesis was described by Tommerup et al. (1974). *B. lactucae* is predominantly heterothallic and two sexual compatibility types (mating types), designated B1 and B2, have been described (Michelmore and Ingram, 1980; Michelmore, 1981). Secondary homothallism may sometimes also occur (Michelmore and Ingram, 1982).

Some detailed studies have focussed on sexual reproduction in populations of *B. lactucae* occurring on cultivated lettuce (*L. sativa*) (Gustafsson et al., 1985; Crute, 1987). However, there is limited information on the distribution of sexual compatibility types in populations of *B. lactucae* occurring on *L. serriola*. Nevertheless, existence of heterothallism and the presence of two mating types (B1 and B2) was demonstrated in *B. lactucae* isolates originating from *L. serriola*, and the occurrence of sexual reproduction based on crossing of isolates originating from cultivated lettuce (*L. sativa*) and *L. serriola* described (Lebeda and Blok, 1990).

Detailed research focussed on genetic variation of virulence in the wild pathosystem *L. serriola* – *B. lactucae* has been initiated (Lebeda, 1984, 1998b; Lebeda et al., 1999; Petrželová and Lebeda, 2000, 2001; Lebeda, 2002; Lebeda et al., 2002b), however importance of this phenomenon from the theoretical and practical viewpoint is rather limited (Lebeda, 1989a, b; Lebeda et al., 2002b). The aim of the present paper was to determine mating types in *B. lactucae* isolates originating from populations of *L. serriola* occurring in the Czech Republic and some other European countries, and to evaluate their potential contribution to the genetic variation of virulence in natural populations of this pathogen.

Materials and Methods

Origin of isolates

Fifty-nine isolates of *Bremia lactucae* (Table 1) originating from 33 naturally infected populations of *Lactuca serriola* were used for determination of sexual compatibility types. Most isolates were collected during the year 1998 and 1999 in various types of habitats in the territory of Central and Southern Moravia (districts Brno-country, Olomouc, Prostějov). One isolate that was collected in 1999 originated from Central Bohemia (district Rakovník) (Table 1, Fig. 1). Only four isolates originated from abroad. Two isolates were collected on natural populations of *L. serriola* near Eichelborn (Thüringen, Germany) and two isolates were collected near Mégève (Savoie Alps, France) (Lebeda et al., 2001). Isolates were maintained and multiplied on seedlings of *L. serriola* (LSE/57/15) susceptible to all investigated isolates.

Determination of mating types

Isolates from *L. serriola* were examined for their ability to produce the oospores during co-cultivation with isolates of known mating type. For determination of mating types (B1 and B2), isolates (races) of *B. lactucae* previously described as NL5 (B2 type) and NL12 (B1 type) (Lebeda and Blok, 1990, 1991) were used. Both isolates were maintained and multiplied on seedlings of *L. sativa* cv. Cobham Green.

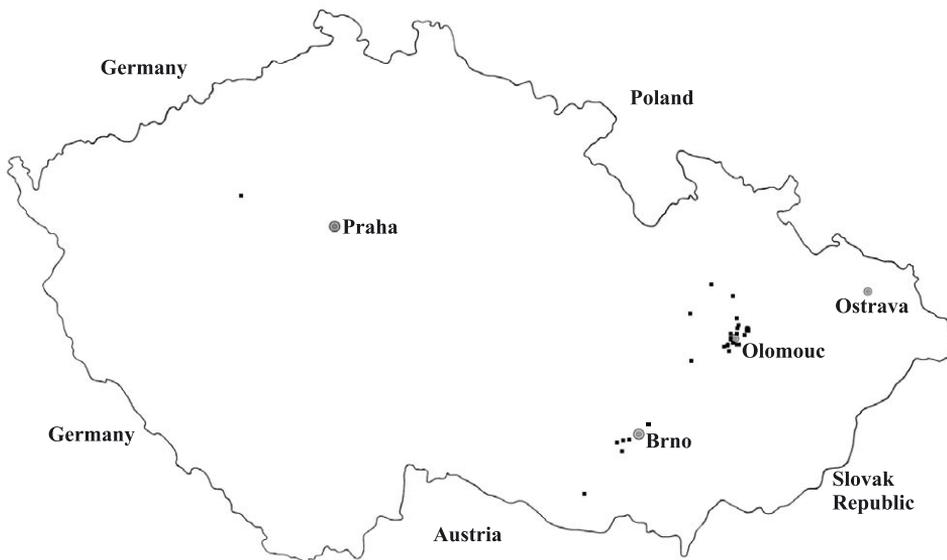


Fig. 1. Collecting sites of *Bremia lactucae* isolates used for mating types determination in the Czech Republic

Table 1

Origin of *Bremia lactucae* isolates from *Lactuca serriola*, their sexual compatibility types and intensity of oospore formation

| Year | Isolate no. | Origin | | Mating type | Oospore formation* |
|-----------------------------|--|-----------------|-----------------------------------|-------------|--------------------|
| | | District | Location | | |
| 1997 | 42/97 | Zn | Lechovice u Znojma | B2 | 0–1 |
| 1998 | 3/1/98, 3/2/98, 3/3/98 | Pv | Soběsuky | B2 | 2–3 |
| | 18/1/98 | Bc | Brno-Hády | B2 | 0–1 |
| | 21/1/98, 21/4/98, 21/5/98 | Bc | Hajany I | B2 | 1 |
| | 22/4/98, 22/10/98 | Bc | Hajany II | B2 | 1–2 |
| | 24/2/98, 24/3/98 | Bc | Ořechov | B2 | 1–2 |
| | 28/1/98, 28/3/98, 28/4/98 | Bc | Rd. Silůvky - Moravské Bránice | B2 | 1–3 |
| | 31/2/98, 31/4/98, 31/5/98, 31/7/98, 31/8/98 | Bc | Pravlov | B2 | 1–2 |
| | 32/98, 33/98 | Ol | Olomouc-Nový Dvůr | B2 | 1–2 |
| | 37/98, 39/98 | Ol | Grygov I | B2 | 1 |
| | 1999 | 4/99 | Ol | Velký Týnec | B2 |
| 5/99 | | Ol | Olomouc-Holice I | B2 | 1–2 |
| 6/99 | | Ol | Olomouc-Nový Dvůr | B2 | 1 |
| 9/99 | | Ol | Krčmaň | B2 | 0–1 |
| 24/99 | | Ol | Přáslavice | B2 | 1–2 |
| 25/99, 26/99, 102/99 | | Ol | Svésladice | B2 | 0–1 |
| 27/99, 28/99 | | Ol | Grygov II | B2 | 2–4 |
| 30/99 | | Ol | Savín | B2 | 1 |
| 65/99 | | Ra | Krupá | B2 | 1–2 |
| 68/99, 68/2/99 | | Ol | Olomouc-Holice II | B2 | 1–2 |
| 81/99 | | Ol | Olomouc-Droždín | B2 | 1–2 |
| 87/1/99 | | Ol | Tážaly | B2 | 1–2 |
| 88/1/99 | | Ol | Bolelouc | B2 | 1–2 |
| 90/1/99 | | Ol | Rd. Vrbátky to Blatec | B2 | 1 |
| 92/99 | | Ol | Rd. Šternberk to Hlásnice | B2 | 1–2 |
| 93/1/99, 93/2/99, 93/3/99 | | Ol | Horní Sukolom | B2 | 1–2 |
| 95/1/99, 95/2/99 | | Ol | Olomouc-Holice III | B2 | 1–2 |
| 96/1/99, 96/2/99 | | Ol | Grygov II | B2 | 1–3 |
| 97/1/99 | | Ol | Rd. Grygov to Blatec | B2 | 1 |
| 98/99 | | Ol | Blatec | B2 | 1 |
| 103/99 | Ol | Near Bystrovany | B1 | 1 | |
| 104/99 | Ol | Near Bystrovany | B1/B2 | 0–1/0–1 | |
| 105/99 | Ol | Near Mrsklesy | B2 | 1 | |
| Isolates from abroad | | | | | |
| 1999 | 66/99, 67/99 | | Eichelborn (Germany) | B2 | 1–2 |
| | 83/99, 84/99 | | near Mégève (France) | B2 | 0–1 |

Abbreviations:

Rd. – Road, Bc – Brno-country, Ol – Olomouc, Pv – Prostějov, Ra – Rakovník, Zn – Znojmo

Intensity of oospore formation:

0 = none; 1 = sparse; 2 = medium; 3 = abundant; 4 = very abundant

* Values represent average of 5 (or 10) leaf discs

Experiments used leaf discs (10 mm in diameter) of *L. serriola* (LSE/57/15) susceptible to all isolates investigated. Leaf discs were taken from the leaves of adult plants 10 weeks after transplantation and were placed with their abaxial side upwards in Petri dishes (90 mm) on moistened filter paper. Five leaf discs or segments of approximately the same size were included in one test. Tests were carried out separately with B1 and B2 types.

Inoculum of *B. lactucae* races NL12 and NL5 and the tested isolate was prepared by washing spores from seedlings with distilled water, and the density adjusted to give ca 10^5 spores ml^{-1} . Leaf discs were inoculated with a pipette on their abaxial surface. Each disc received 10 μl of the conidial suspension of the test isolate plus 10 μl of either NL12 or NL5 isolate (B1 or B2 mating type), and the two suspensions were mixed. Inoculated leaf discs were incubated at a temperature of 10 to 15 °C under a 12 h photoperiod. Thirteen days after inoculation, leaf discs were fixed and decolourized in 100% acetic acid (glacial) for 24 h and then stored in glycerol for subsequent evaluation (Lebeda and Blok, 1990). The presence or absence of oospores (Fig. 2) was verified microscopically (100 \times magnification) and quantified using a 0–4 scale (Table 1).

Evaluation of natural occurrence of oospores

Naturally infected leaves were collected from *L. serriola* plants during 1999 and 2000 at the 15 localities within the evaluated area from which the studied isolates of *B.*

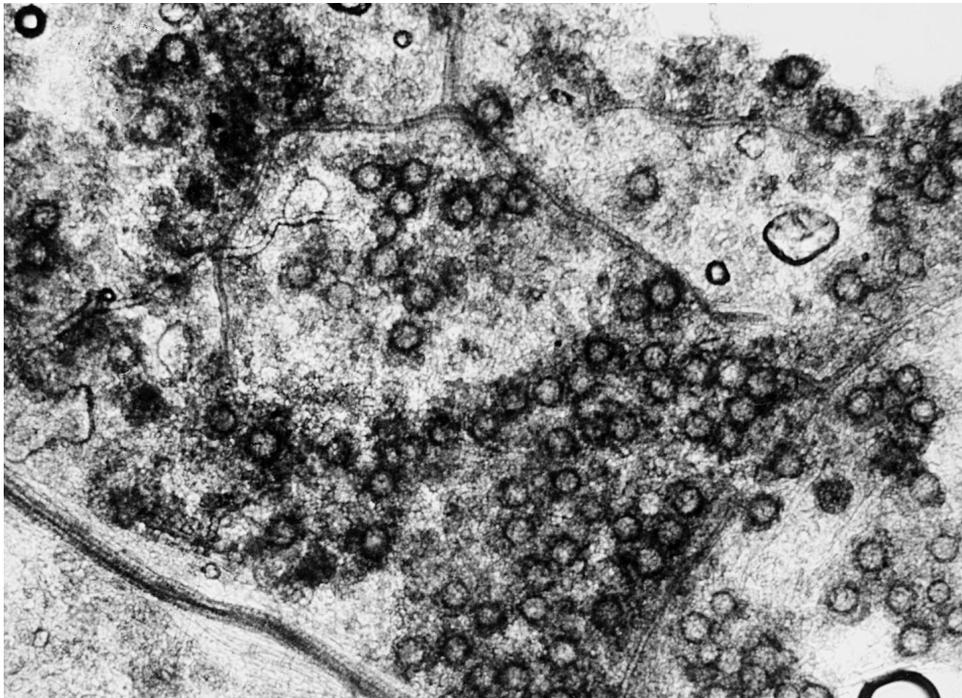


Fig. 2. Abundant formation of *Bremia lactucae* oospores

lactucae originated. Leaves with visible symptoms of infection were cut into pieces of ca 20 × 20 mm. Leaf segments were treated by the same way as described above for the leaf discs, and they were evaluated for the natural occurrence of oospores.

Results and Discussion

All 59 isolates of *B. lactucae* from *L. serriola* were able to produce oospores when co-cultivated with either isolate NL5 (B2) or NL12 (B1). The results obtained for each isolate and their place of origin are summarized in *Table 1*.

Both sexual compatibility types (B1 and B2) were recorded. One isolate collected in year 1997 produced a few oospores in combination with NL12 (B1), and was therefore a B2 sexual compatibility type. All twenty-three isolates collected in 1998 formed oospores (sparse to abundant intensity) when cultivated together with NL12 and were designated as B2 type. A similar situation was recorded in the set of isolates collected in 1999, with the majority collected in the Czech Republic and assessed as a B2 type. Only one isolate (103/99) produced oospores in combination with isolate NL5, indicating that this isolate was B1 mating type (*Table 1*). There was also one other isolate producing a few oospores with both B1 and B2. The isolates originating from France and from Germany were assessed as B2 mating type (*Table 1*). In total 96,4% of the isolates represented B2, and only 3.6% B1 (*Table 2*).

Table 2

Summary of the occurrence of mating types in populations of *Bremia lactucae* on *Lactuca serriola*

| Year | Total number of isolates tested | No. of isolates producing oospores with race NL12 (B1); mating type B2 | No. of isolates producing oospores with race NL5 (B2); mating type B1 |
|-------------------------------|---------------------------------|--|---|
| Czech Republic | | | |
| 1997 | 1 | 1 | 0 |
| 1998 | 23 | 23 | 0 |
| 1999 | 31 | 29 + 1* | 1 + 1* |
| <i>Total:</i> absolute values | 55 | 53 + 1* | 1 + 1* |
| percentage (%) | 100 | 96.4* | 3.6* |
| France | 2 | 2 | 0 |
| Germany | 2 | 2 | 0 |
| <i>Total:</i> absolute values | 4 | 4 | 0 |
| percentage (%) | 100 | 100 | 0 |

* One isolate produced oospores both with NL12 (B1) and NL5 (B2).

The natural occurrence of oospores of *B. lactucae* in naturally infected leaves of *L. serriola* was investigated in 40 samples originating from 15 localities, but no oospores were found. In leaves originating from one locality (near Olomouc-Nové Sady) a very sporadic occurrence of developing oogonia and antheridia was recorded.

The capability to form oospores (Fig. 2) was proved experimentally in all recently tested isolates of *B. lactucae* originating from *L. serriola*. This confirms previously published results obtained from a limited set of isolates originating from a small number of localities (Lebeda and Blok, 1990). However, mating type determination was not unambiguous in all leaf discs included in the recent tests. In some leaf discs oospores were not detected or the intensity of oospore formation was low (Table 1). Infection of these discs was successful and profuse asexual sporulation was recorded. In numerous fungi, including *B. lactucae*, an inverse relationship between occurrence of sexual and asexual reproduction has been reported (Michelmore, 1981; Chamberlain and Ingram, 1997). Further reason for only sparse production of oospores in some combinations of B1 and B2 isolates could be based on isolate differences. Experiments with *Phytophthora infestans*, an other heterothallic oomycete, showed that some combinations of the two mating types were more capable of forming oospores than others (Flier et al., 2001). For our studies, isolates of *B. lactucae* originating from two related host species (*L. sativa* and *L. serriola*) were used. Recent results may indicate that isolates of one pathogen originating from different host species do not need to be completely compatible when pairing together to produce oospores.

In total, 58 of the isolates analyzed were exclusively B1 or B2 mating type. Prevalence of mating type B2 has been demonstrated in recent natural populations of *B. lactucae* found in the Czech Republic. Our present results are consistent with some previous reports on oospore formation (Michelmore and Ingram, 1980; Michelmore, 1981; Lebeda and Blok, 1990). Existence of both mating types, with prevalence of B1 type, was recorded in German populations of *B. lactucae* on cultivated lettuce (Lebeda, 1997; Lebeda and Zinkernagel, 2002). Detailed studies of Swedish populations of *B. lactucae* on lettuce demonstrated frequent occurrence of sexual reproduction (ca 60%) and presence of both mating types, sometimes on the same host plant (Gustafsson et al., 1985). Only two isolates (3.6%) in the present study were able to form oospores in combination with B2 and thus been classified as B1 type. From the viewpoint of the geographic distribution, B1 mating type isolates (103/99 and 104/99) were recorded at only one site (Table 1), where the populations of *L. serriola* were growing close to each other (about 1 km apart). One of these isolates produced oospores in combination with both B1 and B2. This result is similar to those reported by Lebeda and Blok (1990) for one isolate (4/82). In relation to this isolate, the potential occurrence of secondary homothallism (Michelmore and Ingram, 1982) was discussed (Lebeda and Blok, 1990). Nevertheless, we can conclude that the mating type B2 is generally dominant within the whole pathogen population on *L. serriola*. However, more detailed information about mating type distribution in the crop pathosystem occurring in the same territory is not available, and needs further investigation.

Sexual reproduction is considered to be the most important source of virulence variation in populations of *B. lactucae* (Gustafsson et al., 1983, 1985; Lebeda and Blok, 1990; Crute, 1992). It is however questionable, how the two sexual compatibility types participate in generating this variation, when populations of this heterothallic fungus are represented in high frequency by only one mating type. Distribution of mating types was studied in populations of the heterothallic oomycete *P. infestans*, and disequilibrium in occurrence of the two mating types A1 and A2 in various regions was recorded frequently (Fraser et al., 1999; Daayf et al., 2000). Furthermore, it seems that mating types A1 and A2 are mostly separated geographically (Goodwin et al., 1995). The occurrence of only one mating type of *P. infestans* for a long time in some areas resulted in asexual reproduction of these populations (Goodwin et al., 1995; Jaime-Garcia et al., 2000), while sexual reproduction occurred only in areas where isolates of both mating types co-existed (Sujkowski et al., 1994; Goodwin et al., 1995). In the light of these facts, the importance of sexual recombination as the main factor generating variation in recent Czech populations of *B. lactucae* on *L. serriola* is questionable. It is possible that a situation similar to the A1 and A2 distribution in populations of *P. infestans* also exists in populations of *B. lactucae*, and there may be a geographic separation of isolates of the two mating types (B1 and B2). However, mating types have not been determined yet in all Czech populations of *B. lactucae* on *L. serriola*, so we cannot deduce any general conclusions about the contribution of sexual reproduction to the genetically based virulence observed in the Czech Republic.

Our recent observations clearly document that natural occurrence of sexual reproduction is quite rare in populations of *B. lactucae* on *L. serriola*. This finding differs from that published for the *L. sativa* – *B. lactucae* crop pathosystem, where sexual reproduction and recombination frequently occur and account for the pathogen virulence structure and changes (Gustafsson et al., 1983, 1985). Why these differences in sexual reproduction between wild and crop pathosystems occur should be investigated.

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