LIFE CYCLE AND GENETIC DIVERSITY OF WILLOW RUSTS
(*Melampsora* spp.) IN EUROPE

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Abstract

The paper is a review of classical and recent studies on willow rusts in Europe, with special reference to short rotation coppice willows used for biomass production, such as common osier willow (*Salix viminalis* L.). The review presents the taxonomic classification of rust fungi from the genus *Melampsora* spp. We present a list of telial hosts (genus *Salix*) as well as aecial hosts for different rust species. The life cycle of this fungal pathogen is described in detail from the epidemiological and genetic point of view. The DNA polymorphism of *M. larici-epitea*, the rust species most responsible for severe yield losses of plant biomass, is characterised based on RAPD, AFLP and RFLP-PCR methods.

Key words: willow, *Salix* sp., rust, *Melampsora* spp., life cycle, genetic diversity, short rotation coppice

INTRODUCTION

The leaf rust, caused by *Melampsora* spp., is the most widespread and frequent disease of biomass willows (*Salix*), planted for renewable energy, in many parts of Europe (P e i et. al. 1999; S a m i l s, 2001; M c C r a c k e n and D a w s o n, 2003; R ö n n b e r g - W ä s t l j u n g et al. 2008; P r z y - b o r o w s k i and S u l i m a, 2010). It can defoliate willows and predisposes them to other diseases. In extreme cases, it can reduce yield as much as 40% (P a r k e r et. al. 1993). The willow rust, one of the most important limiting factors for biomass productivity, is well established in the UK, and all countries of Western Europe – especially in Sweden where willow biomass production fields are frequent. The fungi of the genus *Melampsora* are damaging agents for willows in Poland (R e m l e i n - S t a r o s t a, 2007; J e - d r y c z k a et. al. 2008). As the green energy is projected to make an important contribution to the future energy (S z c z u k o w s k i et al. 2005; T r y b u s h et al. 2008), the study of its pathogens is regarded as significant.

CLASSIFICATION OF RUST FUNGI

The rust fungi belong to the class Pucciniomycetes and the order Pucciniales. They contain about 7,000 species (W e b s t e r and W e b e r, 2007), which are grouped in more than 100 genera (C u m m i n s and H i r a t s u k a, 1983; Ono and Aime, 2006). The popular name "rust fungi" refers to the reddish – brown colour of urediniospores which are produced in dense pustules on the host plant surface (leaf or stem), giving them a "rusted" appearance.

The rust fungi are unique in many aspects. They are biotrophs, i.e., they can thrive only on the living tissue of plants. Their life cycle is complex, consisting of five spore stages (Fig. 1). They are either heteroecious or autoecious. Heteroecoius species infect two plant hosts which are taxonomically unrelated to each other. Autoecious species, on the other hand, complete their life cycle on the same plant host. A significant feature of these fungal species is their host specificity, i.e., a specific group of rust is capable of infecting a certain range of plant species (P e i et al. 2005).

The rust fungi cause diseases on a wide range of plant species, including trees (e.g., willow, poplar, pine, apple, coffee), cereals (e.g., wheat, oats, barley), vegetables (e.g., bean, asparagus), other field crops (e.g., cotton, soybean), and ornamentals (e.g., carnation, chrysanthemum, snapdragon) (A g r i o s, 2005).

The taxonomy of the rust fungi bases on teliospore morphology, however it has been changing throughout the years. At first, four families were distinguished within the order Uredinales (now: Pucciniales). Later, the number of families was reduced to two:

Melampsoraceae and Pucciniaceae. C u m m i n s and H i r a t s u k a (1983, 2003) proposed a 13- to 14-family system. In their system, only the genus Melampsora is included in the family Melampsoraceae.

TAXONOMY OF WILLOW RUST

The genus *Melampsora* was established by C a s t a g n e in 1843 (cited by P e i , 2005). The main characteristic of the genus *Melampsora* is the formation of a subepidermal crust of sessile, single-celled teliospores, which are visible as black spots on the host's leaf surface (gr. melas – black, psora – scab). The genus *Melampsora* contains 80-100 species and more than half have been described on Salicaceae. Of the 51 species introduced by S y d o w and S y d o w (1915), 10 were found on poplars (*Populus*) and 22 on willows (*Salix*), both belonging to Salicaceae (P e i , 2005). The most of *Melampsora* species causing willow and poplar rusts are heteroecious. Heteroecious rust species alternate usually on conifers, but also on dicotyledonous and monocotyledonous plants (P e i , 2005). Alternate hosts for the genus *Melampsora* fungi have been described by G ä u m m a n (1959), and they are as follows: *Abies, Allium, Euonymus, Larix, Ribes, Saxifraga, Viola*, and some species of Orchidaceae. The majority of autoecious fungi of *Melampsora* spp. occur on dicotyledonous plants (e.g. Euphorbiaceae and Linaceae) (P e i et al. 2005), and there is one autoecious species, *M. amygdalinae* Kleb., which occurs on willow plants (S y d o w and S y d o w , 1915; G ä u m m a n , 1959). It was proved that the occurrence of an alternate host adjacent to the primary willow host caused earlier and more severe rust attacks (S a m i l s et al. 2001b).

The taxonomy of fungal species belonging to *Melampsora* spp. is unclear. Within willow rust species, special forms and pathotypes can occur, each capable of infecting certain group of willow plants (P e i et al. 1996; S a m i l s et al. 2003). Moreover, the occurrence of these special forms and pathotypes may vary between geographical regions (P e i et al. 1999). Many rust species were described in the late 19th to early 20th century and they were established based on their morphology, alternate host and the telial host range (G ä u m m a n , 1959; L e p p i k , 1972; S a v i l e , 1976; C u m m i n s and H i r a t s u k a , 2003). The fact that host ranges of different rust species often overlap and that these species are indistinguishable in morphology, causes many difficulties in proper identification of *Melampsora* species. G ä u m m a n (1959) proposed a taxonomic system that regards rust fungi with different alternate hosts as distinct species. H y - l a n d e r et al. (1953) recognized *Melampsora epitea* Thüm. as a complex species to include species of similar morphology. Another system created by W i l s o n and H e n d e r s o n (1966), based on Hylander's system, gathers various species and races that are similar in morphology, but alternate on hosts of different genera, into one collective species – *M. epitea* Thüm.

HOST GENUS *SALIX*

Willows (*Salix* L.) belong to the family of Salicaceae. The genus *Salix* is one of the largest in the northern hemisphere, as regards woody plants. The number of described willow species varies between 300 – 500 worldwide, with 270 species in China, 120 in the former Soviet Union, over 100 in North America, and some 65 willow species in Europe (A r g u s , 1997; P e i , 2005). *Salix* species are insect-pollinated dioecious plants, which hybridize relatively easily. This is the most probable reason of taxonomic difficulties. Willows are grouped into subgenera, such as *Vetrix* (shrub willows), *Chamaetia* (dwarf willows), and *Salix* (tree willows). As far as there is an agreement among taxonomists on the recognition of species typically forming trees (*Salix*), the classification of willows of the subgenera *Vetrix* and *Chamaetia* is problematical, because they differ widely in their morphology. Almost all willows planted for biomass production belong to the subgenus *Vetrix*, which consists of 1520 species (P e i et al. 1996).

LIFE CYCLE

The life cycle of the fungi belonging to the genus *Melampsora* is complex, including five different spore stages, i.e., basidiospores, spermatia, aecciospores, urediniospores, and teliospores (Fig. 1). It is probably the most complex life cycle found anywhere in nature (W e b s t e r and W e b e r , 2007).

The spread of rust on a willow host takes place during the summer and includes several repeated cycles of clonal propagation of urediniospores. The urediniospores are capable to produce the next generation in 6-7 days (P e i et. al. 1996). The fungus develops teliospores in late summer and autumn, and overwinters on fallen willow leaves. In the spring, they germinate to produce basidiospores which are capable to infect the alternate host – larch (*Larix*), on which asexual reproduction takes place. Fertilization between spermatia and receptive hyphae results in the formation of recombinant aecciospores. The aecciospores infect new willow leaves in the early summer, and in this way the life cycle is completed. The spore stages differ, according to their nuclear condition. The basidiospores and spermatia are monocarytotic, containing a single haploid nucleus (1n), while aecciospores and urediniospores are dikaryotic, having two haploid nuclei (1n + 1n). The teliospores are dikaryotic in the early phase, but later the two nuclei fuse (2n) forming a diploid cell (Fig. 2).
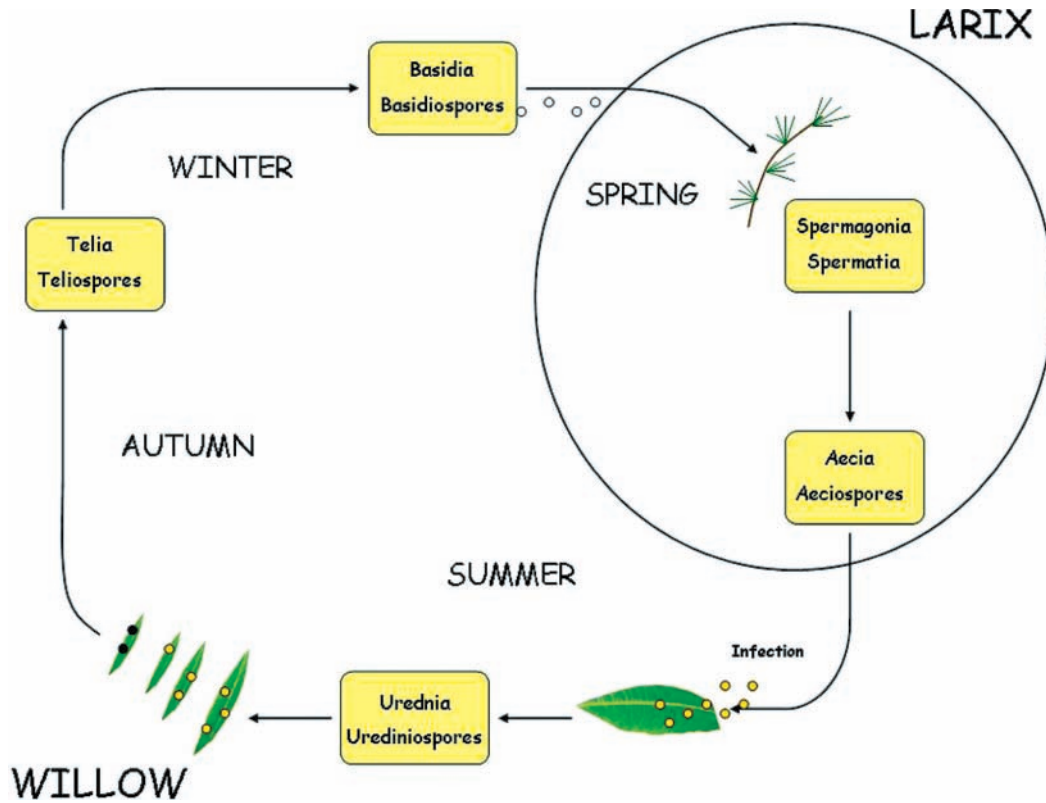
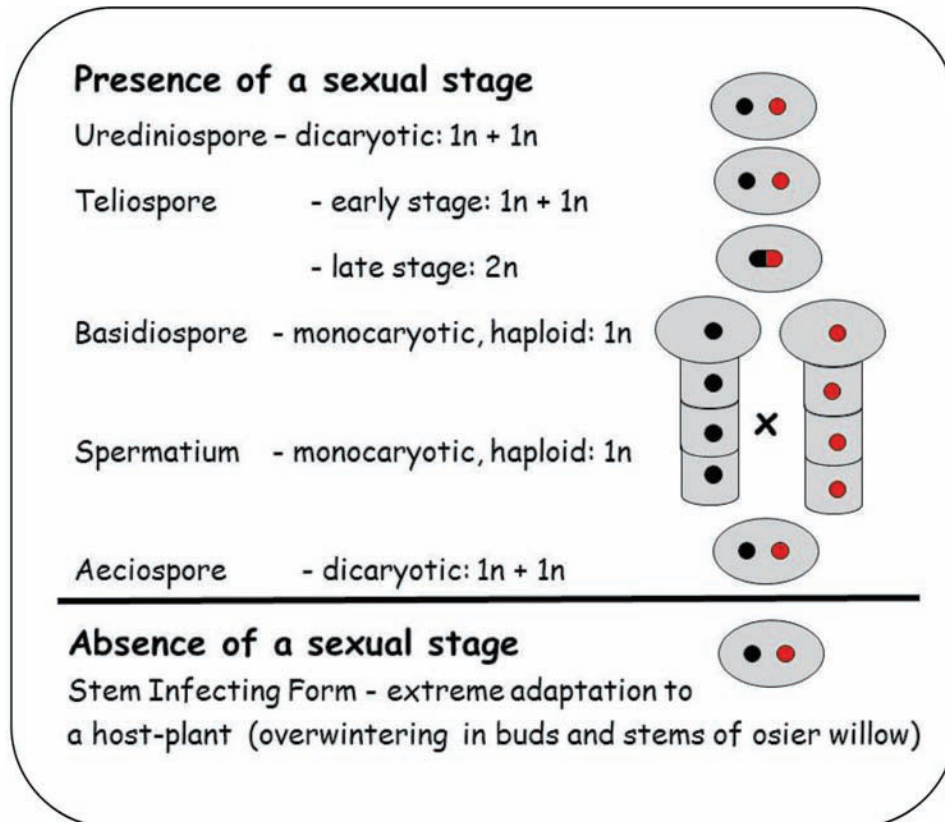Fig. 1. The life cycle of *Melampsora* spp.

Fig. 2. Nuclei of *Melampsora* spp. at different stages of the fungus life cycle

RUSTS SPECIES
ON WILLOW PLANTS

Of all willow species, the most popular in biomass plantations is common osier willow *S. viminalis* and its numerous interspecific hybrids. S z c z u k o w - s k i et al. (2004) mention two other willow species that can be grown for energy production, considering their quick biomass increase, i.e. *S. amygdalina* (syn. *S. triandra*) and *S. dascyclados* (syn. *S. burjatica*). Besides, there are some other important species of willows that can be successfully planted in short-rotation coppice, i.e. *S. caprea, S. cinerea, S. daphnoides* and *S. purpurea*.

There are many species of *Melampsora* spp. that were described on willows in Europe (Table 1). Of the 34 rust species identified worldwide, 18 were described on willow plants on the Old Continent. By now, the predominant leaf rust in willow plantations has been *M. larici – epitea* (the larch alternating group of *M. epitea* var. *epitea*) (P e i et al. 1993). Within *M. larici – epitea*, six *formae speciales* have been recognized in Europe: f.sp. *larici – epitea typica* Kleb., f.sp. *larici – daphnoides* Kleb., f.sp. *larici – nigricantis* Schneid.,

f.sp. *larici – purpurea* Schneid., f.sp. *larici – retusae* Fischer, f.sp. *larici – reticulate* (S y d o w and S y - d o w , 1915; G ä u m m a n , 1959). *M. larici – epitea* was observed on several willow species, i.e. *S. aurita, S. caprea, S. cinerea, S. daphnoides, S. dascyclados, S. purpurea, S. triandra,* and *S. viminalis*, but only one of six special forms was identified as capable to infect osier willow (*S. viminalis*) - f.sp. *larici – epitea typica*. Simultaneously, f.sp. *larici – epitea typica* was found on other willow species (*S. aurita, S. caprea, S. cinerea*) (cited by P e i , 2005). Recent data obtained in Poland also confirm that *M. larici – epitea* f.sp. *typica* is a dominant pathogen of *S. viminalis* in the country (C i s z e w s k a - M a r c i n i a k et al. 2010). The willow species infected by other special forms of *M. larici – epitea* are listed in Table 1. *M. ribesii – viminalis* Kleb. and Stem Infecting Form (SIF) were observed on common osier willows in the UK (P e i , 2005). The first one alternates on *Ribes* spp. and the second one is deprived of a sexual stage in its life cycle (P e i et al. 1993, 1995). Within *Melampsora* species, mentioned in Table 1, *M. amygdalinae* Kleb. is the only one autoecious willow rust (no alternate host is required).

Table 1
The list of *Melampsora* species reported on the most popular willows in Europe,
including these used for biomass production*

Willow species (*Salix* spp.) Telial host	Aecial host	Rust species (*Melampsora* spp.)
S. alba	*Alliums* spp.	*M. salicis-albae* Kleb. (= *M. allii-salicis-albae* Kleb.)
S. aurita	*Abies* spp.	*M. abieti-caprearum* Tubeuf. (= *M. humboldtiana* Speg.)
	Euonymus europaeus	*M. euonymi-caprearum* Kleb. f.sp. *typica* Kleb.
	Larix spp.	*M. larici-caprearum* Kleb. (= *M. caprearum* Thüm.) f.sp. *grandifoliae* Schneid.
	Larix spp.	*M. larici-epitea* Kleb. f.sp. *larici-epitea typica* Kleb.
	Ribes spp.	*M. ribesii-epitea* Kleb. f.sp. *ribesii-auritae* Kleb.
	Ribes alpina	f.sp. *ribesii-grandifoliae* Schneid.
S. caprea	*Abies* spp.	*M. abieti-caprearum* Tubeuf. (= *M. humboldtiana* Speg.)
	Larix spp.	*M. larici-caprearum* Kleb. (= *M. caprearum* Thüm.) f.sp. *typica* Kleb. f.sp. *grandifoliae* Schneid.
	Euonymus europaeus	*M. euonymi-caprearum* Kleb. f.sp. *typica* Kleb.
	Larix spp.	*M. larici-epitea* Kleb. f.sp. *larici-epitea typica* Kleb.
S. cinerea	*Abies* spp.	*M. abieti-caprearum* Tubeuf. (= *M. humboldtiana* Speg.)
	Euonymus europaeus	*M. euonymi-caprearum* Kleb. f.sp. *typical* Kleb.
	Larix spp.	*M. larici-epitea* Kleb. f.sp. *larici-epitea typica* Kleb.

S. daphnoides	*Larix* spp.	*M. larici-epitea* Kleb. f. sp. *larici-daphnoides* Kleb. f. sp. *larici-purpureae* Schneid.
S. dascyclados	*Larix* spp.	*M. larici-epitea* Kleb. f.sp. *larici-retusae* Fischer
S. fragilis	*Alliums* spp. *Galanthus nivalis*	*M. allii-fragilis* Kleb. *M. galanthi-fragilis* Kleb.
S. purpurea	*Abies* spp. *Larix* spp. *Ribes* spp.	*M. abieti-caprearum* Tubeuf. (= *M. humboldtiana* Speg.) *M. larici-epitea* Kleb. f.sp. *larici-purpureae* Schneid. *M. ribesi-purpureae* Kleb.
S. triandra	*S. triandra,* *S. pentandra*	*M. amygdalinae* Kleb.
S. viminalis	*Larix* spp. *Ribes* spp. No known aecial stage	*M. larici-epitea* Kleb. f.sp. *larici-epitea typica* Kleb. *M. ribesi-viminalis* Kleb. Stem-infecting form

* S y d o w and S y d o w, 1915; G ä u m m a n, 1959; W i l s o n and H e n d e r s o n, 1966; P e i et al. 1995; P e i et al. 1996; P e i, 2005; S a m i l s, 2001; C i s z e w s k a - M a r c i n i a k et al. 2010

GENETIC DIVERSITY
IN POPULATIONS OF
MELAMPSORA LARICI – EPITEA

The studies of genetic diversity of plants or animals were possible for a long time before the discovery of nucleic acid structure and DNA/RNA testing methods. However, for microscopic fungi, especially biotrophs, such as rusts, indirect phenotypic observations of their mycelium and fruiting bodies had limited application. The development of Polymerase Chain Reaction method by M u l l i s and F a l o o n a (1987) made possible to amplify specific DNA sequences, which brought in turn the development of numerous techniques to study its diversity in size and nucleotide sequences. An important region studied by numerous researchers was the Internal Transcribed Spacer (ITS) containing two variable non-coding regions nested within the rDNA repeats between the highly conserved small and large subunits of rRNA genes (W h i t e et al. 1990). Numerous studies have shown that the ITS region was highly variable among fungal species, whereas – with some exceptions – the intraspecific variation was low. The first primers designed to amplify the ITS region were nonspecific, however G a r d e s and B u r n s (1993) – followed by other researchers – designed primers with enhanced specificity for basidiomycetes, allowing to study mycorrhizal fungi and rusts. The Restriction Fragment Length Polymorphism (PCR-RFLP) analysis of the ITS region, allowing to divide this region into smaller fragments, using the restriction enzymes, allowed to differentiate some *Melampsora* rust species originating from willows into ten groups, with six groups being species-specific (N a k a m u r a et al. 1998). The isolates of *M. epitea* were separated into three RFLP types, suggesting that it is a complex composed of at least three distinct species or sub-species.

One of the popular methods to study the DNA polymorphism is the use of Random Amplified Polymorphic DNA, which does not demand any knowledge on the sequence of the studied DNA fragment. Using this method, it was possible to distinct between stem- and leaf-infecting forms of *Melampsora* rust on osier willow (P e i et al. 1997). Another widely used method allowing to study the DNA polymorphism of *M. larici-epitea* was Amplified Fragment Length Polymorphism. The method allowed to find distinct DNA profiles in morphologically similar isolates (S a m i l s et al. 2002). Moreover, AFLP helped to assess the genetic structure of its populations in different countries. The method revealed high levels of gene and genotypic variation in Swedish populations (S a m i l s et al. 2001a). High genetic variation was observed even within isolates originating from one field. The result suggested the importance of sexual reproduction in rust fungi present in this region. However, no differences in genetic composition were found in *M. larici-epitea* populations obtained from monoclonal and mixed willow fields (S a m i l s et al. 2003). Extremely high gene and genotypic diversity observed in Sweden contrasted with low DNA polymorphism of isolates originating from Northern Ireland (S a m i l s et al. 2001b).

In 2006 fifteen microsatellite loci were described in the poplar rust fungus, *M. larici-populina,* and five related species (B a r r è s et al. 2006), but they have not been found in *M. larici-epitea* by now.

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Cykl życiowy i zmienność genetyczna rdzy (*Melampsora* spp.) na wierzbach w Europie

Streszczenie

Publikacja zawiera przegląd najważniejszych, a także najnowszych badań dotyczących rdzy na wierzbach w Europie, ze szczególnym uwzględnieniem wierzb krzewiastych o krótkiej rotacji, takich jak wierzba wiciowa (*Salix viminalis* L.), stosowanych w celu uzyskania biomasy roślinnej. W pracy przedstawiono listę gatunków rodzaju *Melampsora* spp., powodujących rdze na wierzbach. Praca zawiera spis wierzb (rodzaj *Salix*), na których powstają telia oraz różnych gatunków roślin – gospodarzy dla stadium tworzenia ecjów. Z epidemiologicznego i genetycznego punktu widzenia opisano cykl życiowy tych patogenów grzybowych. Zaprezentowano także wyniki badań nad polimorfizmem DNA, charakteryzowanym metodami RAPD, AFLP oraz RFLP-PCR u *M. larici-epitea*, gatunku rdzy odpowiedzialnego za największe straty plonu biomasy wierzby.