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Melampsora rust species on biomass willows in central and north-eastern Germany



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ABSTRACT

Melampsora willow rusts are the most important fungal pathogens in short rotation coppices of biomass willows. In the past, breeding programmes for rust resistant biomass willows concentrated on the distinction of races within the forma specialis *Melampsora larici-epitea* f. sp. *larici-epitea typica* that colonized *Salix viminalis* and related clones. In a new breeding program that is based on a wider range of willow species it is necessary to identify further *Melampsora* species and formae specialis that are pathogens of willow species other than *S. viminalis*. Therefore, three stock collections with *Salix daphnoides*, *Salix purpurea*, and other shrub willow species (including *S. viminalis*) species were sampled in north-eastern Germany. A fourth stock collection in central Germany contributed rusts of tree willows (*Salix fragilis* and *Salix alba*) and the large shrub *Salix caprea*. Out of 156 rust samples, 149 were successfully sequenced for ITS rDNA. A phylogenetic analysis combining Neighbour-Joining, Maximum-Likelihood and Bayesian analysis revealed six species: *Melampsora ribesii-purpureae*, *Melampsora allii-salicis-albae*, *Melampsora* sp. aff. *allii-fragilis*, *Melampsora larici-pentandrae*, *Melampsora larici-caprearum*, and *Melampsora larici-epitea*. The first four species were found exclusively on the expected hosts. *Melampsora larici-caprearum* had a wider host range comprising *S. caprea* and *S. viminalis* hybrids. *Melampsora larici-epitea* can be further differentiated into two formae speciales. The forma specialis *larici-epitea typica* (59 samples) colonized *Salix viminalis* clones, *Salix purpurea*, *Salix dasyclados*, and *Salix aquatica*. In contrast to this relatively broad host range, f. sp. *larici-daphnoides* (65 samples) was found exclusively on *Salix daphnoides*. With the distinction and identification of the rust species/formae speciales it is now possible to test for race-specific resistances in a more targeted manner within the determined pairings of rust and willow species.

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Introduction

Salix (willow) species grow rapidly and produce large amounts of biomass in a short time. Therefore, they are suitable for growing in short rotation coppices (SRC) in order to supply renewable material for energy generation (Makeschin 1999; Strohm et al. 2012). The *Salix* species belong to the family Salicaceae, which also includes the genus *Populus*. *Salix* species have worldwide distribution and are divided into three subgenera (Skvortsov 1999): *Salix* (trees and large shrubs), *Vetrix* (shrubs and small trees), and *Chamaetia* (dwarf willows). The shrub willows can be planted in SRC and have been the subject of different selection and breeding programs for biomass production (Boelcke 2006; Lindegaard et al. 2001; Lindegaard & Barker 1997). One of the aims of biomass willow breeding is the selection of rust resistant lineages (Pei et al. 2008). Rust on *Salix* is a foliar disease that is caused by fungal pathogens of the genus *Melampsora*. Infection by *Melampsora* spp. causes leaf damage, which reduces the effective leaf area and results in lower photosynthetic performance and eventually in defoliation. This can lead to a substantial deficit in biomass yield (Pei et al. 2004).

Apart from *Melampsora amygdalinae*, all *Melampsora* species that infect willows are heteroecious. This means that the fungus needs an alternate host to complete its life cycle. Corresponding to the ploidy level of the fungus, willow species are hosts for the dikaryotic stages of the fungus (uredinia, telia), while the haploid stages (spermogonia, aecia) can be found on hosts in different lineages of seed plants, e. g., *Allium* spp., *Ribes* spp., and *Larix* spp. (Ciszewska-Marciniak & Jedryczka 2011; Pei 2005; Pei et al. 1993). In the past, the distinction of *Melampsora* species relied on spore morphology and determination of host species (Gäumann 1959; Klebahn 1903, 1904; Pei et al. 1993). Below the species level, inoculation tests with aeciospores and uredospores were used to differentiate formae speciales (Klebahn 1904; Pei et al. 1996; Ramstedt et al. 2002; Schneider 1906). First proposed to subdivide cereal rusts of the genus *Puccinia* (Eriksson 1894), the concept of formae speciales is widely used to distinguish fungal pathogens that have the same morphology but colonize different hosts within sharply circumscribed host ranges (Anikster 1984; Reignault & Sancholle 2005; Schulze-Lefert & Panstruga 2011). The concept of formae specialis is closely linked to the concepts of nonhost resistance and basic compatibility: A forma specialis of a pathogen is thought to overcome the basic resistance (or nonhost resistance) of a plant species by establishing basic compatibility between host and pathogen (Prell 1996). From this follows that a host specific forma specialis is not able to grow on a plant other than the host plant because it is not able to overcome the unspecific nonhost resistance of most other plants (Schulze-Lefert & Panstruga 2011). Within the interaction of a forma specialis and the compatible host plant, individual plants or plant populations can again become resistant against the host specific forma specialis. This is called parasite specific resistance (Heath 1991).

The distinction between basic resistance and parasite specific resistance is of importance in the context of willow breeding. Most biomass willows cultivars are based on clones of *Salix viminalis* and related species (McCracken & Dawson 2003; McCracken et al. 2001). They are mainly colonized by a forma

specialis of the species complex *Melampsora larici-epitea*, namely f. sp. *larici-epitea typica* (Pei et al. 2000). Therefore, most breeding related studies on the genetic variability of biomass willow rusts (e. g., Pei & Ruiz 2000; Pei et al. 2000; Samils et al. 2002; Samils et al. 2001; Samils et al. 2003) have analysed phenomena at the level of parasite specific resistance. Resistant willow clones and different pathotypes within the forma specialis *larici-epitea typica* could be detected by leaf inoculation tests and the molecular method AFLP analysis (=Amplified Fragment Length Polymorphism). However, within the *Melampsora larici-epitea* species complex further formae speciales with different host ranges are known: f. sp. *larici-daphnoides*, f. sp. *larici-purpureae*, f. sp. *larici-retusae*, f. sp. *larici-reticulatae* (Gäumann 1959; Pei 2005). The analysis of the host range of these formae speciales is an analysis of basic compatibilities. Especially for f. sp. *larici-daphnoides*, a narrow host range is assumed. Based on inoculation tests, Klebahn (1900b, 1902) reports only *Salix daphnoides* and the closely related *Salix acutifolia* as hosts for f. sp. *larici-daphnoides*. The concept of basic compatibilities can not only be applied to formae speciales, but also to species of *Melampsora* willow rusts. First, many taxa are treated as different taxonomic ranks by different authors (Bagyanarayana 2005). For instance, the forma specialis *larici-daphnoides* (Gäumann 1959) was first described as a species by Klebahn (1900b). Second, many species have similarly narrow host ranges as formae speciales, e. g., *Melampsora ribesii-purpureae*, *Melampsora allii-fragilis* or *Melampsora allii-salicis-albae* (Gäumann 1959).

In a recent breeding programme for drought tolerant and rust resistant biomass willows, the basic compatibilities of *Melampsora* formae speciales and species are in focus, because the willow species basis is broadened beyond the relatives of *S. viminalis*. This makes it necessary to distinguish a wide spectrum of *Melampsora* species and formae speciales and not only pathotypes within a forma specialis. The basis for the breeding programme is a collection of wild type clones of *S. daphnoides*, *S. purpurea*, and *S. pentandra* (Zander 2010) and a collection of established biomass clones ('Sweden clones': *Salix viminalis* and relatives). With the present study we want to answer two questions. First, we want to establish whether it is possible to identify *Melampsora* willow rusts species on the basis of ITS rDNA sequences and to thereby determine host ranges. Second, we aim to confirm the supposedly narrow host range of *M. larici-epitea* f. sp. *larici-daphnoides* in biomass willow stock collections where many alternative hosts are present.

Material and methods

Selection of sample sites and sample collection

The sites of major interest comprised four stock plantations (Fig 1, Table 1). The two stock collections in Berlin-Dahlem and Zepernick had been established within a project to collect and conserve wild types of *Salix daphnoides*, *S. purpurea*, and *S. pentandra* (Zander 2010). Waldsiedersdorf harbours a collection of established biomass clones ('Sweden clones') but also a variety of further shrub willow species that are potentially suitable as biomass willows in SRC. Since these three stock collections are located in relatively close vicinity to each other,

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