First records of the powdery mildews *Erysiphe platani* and *E. alphitoides* on *Ailanthus altissima* reveal host jumps independent of host phylogeny

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Abstract The tree-of-heaven *Ailanthus altissima* (family Simaroubaceae, order Sapindales) is one of the most invasive neophytes in Europe. The tree originated in China and became invasive worldwide in areas with Mediterranean to temperate climates. As known from other invasive plants, only a few pathogens have been reported from *A. altissima* in Europe, and, to date, powdery mildews on it have been unknown in the European region. Recently, two powdery mildews were found on *A. altissima* during a survey of neomycetes on non-native plants in Switzerland. Because they did not fit with any of the species known to occur on Simaroubaceae in Asia, they were identified by DNA barcoding using sequences of the ITS region of the rDNA, revealing them to be the powdery mildews of plane and oak trees, *Erysiphe platani* and *E. alphitoides*. This is the first record of *E. platani* on a host outside the genus *Platanus* and its family Platanaceae, as well as its order Proteales. In contrast, *E. alphitoides* has been reported to occur on several host families and orders. Host jumps over great phylogenetic distances—such as across plant families and orders—appear to be quite common in biogeographically novel associations between Erysiphales species and plants. The consequences of such host jumps for identity and taxonomic placement of species are discussed here. It is further questioned whether both pathogens are usable as biological control agents against the tree-of-heaven.

Keywords Biological control · DNA barcoding · Erysiphales · Host range · Neomycetes · Neophytes

Introduction

Non-native fungi, so-called neomycetes (Kreisel and Scholler 1994), are the least well-investigated group of neobiota even though they have the potential to harm indigenous flora and fauna. Many neomycetes are associated with similarly introduced plants, from which they can potentially spill over onto indigenous plants (Beenken and Senn-Irlet 2016). In response to this phenomenon, neophytes in particular were checked for fungal infections during a survey of neomycetes on plants in Switzerland, with the aim, among others, to find fungal species potentially suitable for biological control against invasive plants (Beenken and Senn-Irlet 2016). This survey included the tree-of-heaven *Ailanthus altissima* (Mill.) Swingle (Simaroubaceae, Sapindales), which is one of the most common invasive neophytes in Europe. It is native to China and was introduced to Europe and North America in the 1740s where it was often planted as an ornamental urban tree. Later, it became invasive worldwide in areas with Mediterranean to temperate climates (Kowarik and Säumel 2007). In Switzerland, the tree-of-heaven is distributed mainly in the southern areas but also in urban regions north of the Alps. It is also spreading in forest habitats potentially favored by climate warming (Gurtner et al. 2015). In addition to its negative effect on native ecosystems in general (Kowarik and Säumel 2007), the expansion of the tree-of-heaven in mountain forests can reduce their protecting function for humans and infrastructures against rock fall (Knüsel et al. 2015). *Ailanthus altissima* is, therefore, on the “black list” of invasive neophytes in Switzerland (Weber 2013, infoflora.ch).

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Alien plant species can become invasive in a new area when they are released from their natural pathogens and predators in a new environment, resulting in a fitness advantage over native species according to the widely accepted enemy-release hypothesis (e.g., Mitchell and Power 2003; for a contrasting position, see van Kleunen and Fischer 2009). Thus, programs against invasive plants often use specific pathogens from their native range for biological control (e.g., Hajek 2004, Tanner et al. 2015).

Only a few fungi are known to occur on the tree-of-heaven in Europe. While most are unspecific common wood-decaying fungi, some leaf diseases caused by *Verrucillium* spp. and *Cercospora* spp. have been reported (Kowarik and Sämel 2007; Siegrist and Holdenrieder 2016). Powdery mildews (Erysiphales, Ascomycota) occurring on *Ailanthus* or other Simaroubaceae have been almost unknown in Europe, where Simaroubaceae are not indigenous (Braun and Cook 2012; Farr and Rossman 2016). To date, the only such case comes from Klenke and Scholler (2015) who reported a conidial stage of an unidentified *Podosphaera* species on *Ailanthus* in Germany. Braun and Cook (2012) listed four species on *Ailanthus* in Asia: *Erysiphe delavayi* (Pat.) U. Braun & Takam, *E. picrasmicola* U. Braun & S. Takam. (both *Erysiphe* sect. *Uncinula*), *Phyllactinia ailanthi* (Golovin & Bunkina) Y.N. Yu, and *Pseudoidium ailanthi* (Bhagyan. & Ramachar) U. Braun & R.T.A. Cook. Additionally, *E. picrasmae* (Sawada) U. Braun & S. Takam. (*E.* sect. *Microsphaera*) has been reported on *Picrasma*, another genus of Simaroubaceae.

Given the rarity of such powdery mildews, it was unexpected for them to be found on several young trees of *A. altissima* in the cities of Basel and Zurich. However, these Swiss collections could not be assigned to one of the known powdery mildews of *Ailanthus* or other Simaroubaceae following Braun and Cook (2012). Thus, the question arose whether new fungal species had been discovered or whether already known powdery mildews infected the tree-of-heaven via host jumps from other plants outside of Simaroubaceae.

Materials and methods

Morphological analyses Fungal structures were investigated from fresh material in water by light microscopy with $\times 100$, $\times 400$ and $\times 1000$ magnification. Some 10–20 conidia, 5–10 conidiophores and (where present) 5–10 ascomata, so-called chasmothecia, of each collection were measured to determine their size range (following Braun and Cook 2012). For microphotographs and drawings, conidia, conidiophores and chasmothecia were prepared from dried material and mounted in lactic acid using a fine needle (see Beenken et al. 2012).

Molecular analyses Small pieces of leaves ($\sim 5 \times 5$ mm) with fungal infections were dried on silica gel. Total DNA was

extracted from chasmothecia (samples LB10424, LB10725, LB10733) or conidiophores (sample LB10721) scraped off the dried material using NucleoSpin Plant II extraction kits (Macherey-Nagel, Düren, Germany) following the manufacturer's standard protocol for plant tissue. The ITS1-5.8S-ITS2 region of n-rDNA (DNA barcode for fungi; see Schoch et al. 2012) was PCR-amplified and sequenced (following the protocol in Beenken et al. 2012) using the primer ITS1F and ITS4 (Gardes and Bruns 1993; White et al. 1990). Sequences were deposited in GenBank (accession numbers in Table S1 and Fig. 1).

For species identification, ITS sequences were compared with accessions deposited in GenBank by applying the Basic Local Alignment Search Tool (BLAST) using the nucleotide search option (BLASTn) (Altschul et al. 1990).

The alignment of 132 ITS sequences was based on the part of the ITS dataset in Takamatsu et al. (2015) around their “*E. alphonseoides*”, “*E. quercicola*” and “*E. platani*” clades that was complemented with further sequences including the four ITS sequences from *Ailanthus* powdery mildews (Table S1). Alignment was performed using MAFFT v.7.017 (Katoh et al. 2002). There were no ambiguous regions within the resulting alignment that required exclusion from the analysis.

The dataset underwent maximum likelihood-based phylogenetic analysis implemented in RAxML v.7.2.8 (Stamatakis 2006). The analysis assumed a general time-reversible (GTR) model of nucleotide substitution and estimated a discrete gamma distribution (GTRGAMMA option in RAxML) with partitions according to the sub-matrices (ITS1/5.8S/ITS2/LSU), which allowed multiple models of substitution. One thousand runs with distinct starting trees were completed using the rapid bootstrap (BS) algorithm of RAxML (Stamatakis et al. 2008). The resulting phylogenetic ML tree (Fig. 1) was rooted on *E. paeoniae* R.Y. Zheng & G.Q. Chen (cf. Takamatsu et al. 2015) and visualized using the Dendroscope program (Huson et al. 2007).

Results

Two morphologically different powdery mildews occurred on *A. altissima* in Switzerland that were identified using DNA barcoding as follows.

The three samples LB10424, LB10725 and LB10733 bearing chasmothecia and long conidiophores revealed identical ITS sequences. A BLASTn search of these nucleotides showed 100% matches with sequences from *Erysiphe platani* on *Platanus* $\times$ *acerifolia* from Germany (GenBank no. JQ365940, JQ365942) and Italy (JQ365941). They form, together with all *E. platani* sequences, a well-supported clade in the phylogenetic analysis (Fig. 1).

One sample on *A. altissima* (LB10721) had only a conidial stage. Its sequence was 100% identical to sequences from

Fig. 1 Positions of the powdery mildews on *Ailanthus altissima* within the phylogenetic tree of *Microsphaera* lineages of the genus *Erysiphe* (red arrowheads). Maximum-likelihood analysis with RAxML v.7.2.6 recovered from ITS sequence data. Numbers at nodes indicate RAxML bootstrap support >50%. Samples are given with host plant, GenBank accession number and origin (cf. Table S1)

E. alphitoides on *Quercus* spp. in GenBank (e.g., AB292699–AB292705), on *Wisteria* spp. (e.g., KP686267–KP686269), on *Oenothera* (KJ700468), on *Paeonia* (AB257434), on *Mangifera* (AB237795) and on *Sorbaria* (KC489094). However, it is also 100% identical to *E. akebiae* (Sawada) U. Braun & S. Takam. on *Akebia* spp. (LC010075) and *E. wallrothii* (U. Braun & Tanda) U. Braun & S. Takam. on *Vaccinium* spp. (AB015930, LC010088). All these samples appear within the *E. alphitoides* clade of the phylogeny (Fig. 1; Table S1).

The morphological characteristics confirmed the molecular results and the identification of the powdery mildews on *Ailanthus* as *E. platani* and *E. alphitoides* since they match their descriptions found in Braun and Cook (2012).

Erysiphe platani* (Howe) U. Braun & S. Takam. on *Ailanthus altissima

≡ *Microsphaera platani* Howe
(Figs. 2 and 3a)

The mycelium on leaflets hypophyllous or rarely amphigenous, forming dense, white patches of c. 0.5–2 cm in diameter; leaflets often deformed and slightly contorted (as on *Platanus*); hyphae about 4–8 µm wide, hyphal appressoria lobed; conidiophores erect, 1–4(5) septate, up to 240 µm long, 5–9 µm wide, foot-cells straight, 30–95 × 4–7 µm; conidia doliiiform, 30–45 × 15–20 µm; chasmothecia scattered, 100–

120(135) µm in diam.; appendages 6–12, 1–2 times as long as the chasmothecia in diameter, 6–10 µm wide, 0–1 septum close to the base, hyaline, brown at the base, apices 4–5 times dichotomously branched, with curved tips; asci 3–6, obovoid, 40–70 × 30–55 µm, wall 2 µm thick, 3–5 spored; ascospores 20–25 × 12–17 µm.

Vouchers (in ZT): Switzerland, Basel, 47°33'49"N, 7°35'05"E, alt. 250 m, 12 Nov 2015, leg. L. Beenken/10725, GenBank no. **KX086213**; Basel, 47°35'52"N, 7°35'10"E, alt. 250 m, 12 Nov 2015, leg. L. Beenken/10733, GenBank no. **KX086214**; Zurich, 47°22'09"N, 8°30'21"E, alt. 430 m, 13 Oct 2015, leg. L. Beenken/10424, GenBank no. **KX086212**.

Erysiphe alphitoides* (Griff. & Maubl.) U. Braun & S. Takam. on *Ailanthus altissima

≡ *Microsphaera alphitoides* Griff. & Maubl.
(Fig. 3b)

Mycelium on leaflets mainly hypophyllous or rarely amphigenous, forming small, white patches of c. 0.5–1 cm in diameter; leaflets never deformed; hyphae about 4–8 µm wide, hyphal appressoria lobed; conidiophores erect, 1–2 septate, up to 40 µm long, 5–7 µm wide, foot-cells straight, 15–30 × 5–8 µm; conidia cylindrical to doliiform, 25–35 × 10–15 µm; chasmothecia lacking.

Fig. 2 **a** *Erysiphe platani* on *Ailanthus altissima*. **b** Infected leaf with deformations caused by the fungal mycelium. **c** Chasmothecium

Fig. 3 *Pseudoidium* on *Ailanthus altissima*: **a** *Erysiphe platani*; **b** *Erysiphe alphetoides*. ap hyphal appressoria, co conidia, cph conidiophores

Voucher (in ZT): Switzerland, Basel, 47°33'30"N, 7°34'52"E, alt. 270 m, 12 Nov 2015, leg. L. Beenken/10721, GenBank no. **KX375804**

Discussion

Species identity

Both *Erysiphe* species found on *Ailanthus* belong to *Erysiphe* sect. *Microsphaera* and are neomycetes introduced to Europe (Braun and Cook 2012). *E. platani* originates from North America and is a globally distributed neomycete on *Platanus* spp. (Pastirčáková et al. 2014). First records in Europe came from southern Italy in the early twentieth century (Sprenger 1916). From there it reached Ticino in

Switzerland south of the Alps in 1988 (Bolay 2005). Nowadays, it is also common and widely distributed north of the Alps where plane trees are planted (Bolay 2005; Scholler et al. 2012; see current distribution in Switzerland in Senn-Irlet et al. 2016). The presented observations on *A. altissima* are the first records of *E. platani* on a host outside the genus *Platanus*. Plane trees heavily infected by *E. platani* were observed in close vicinity to the infected trees-of-heaven in Zurich and Basel. This likely caused high infection pressure and resulted in a short infection path from the ordinary, natural host to the new host plant. A conspicuous symptom on both hosts was the characteristic deformation of the infected leaves (Fig. 2a, b; Kirschner 2011). The length (up to 200 µm) of the conidiophores (Fig. 3a) was an additional feature of this species that differentiated it from other members of *E.* sect. *Microsphaera* (Braun and Cook 2012).

In contrast, the second powdery mildew on *Ailanthus* did not deform the leaves and had shorter (up to 40 µm) conidiophores (Fig. 3b), a rather common feature in the genus *Erysiphe*. DNA sequencing was, therefore, indispensable for its unequivocal identification as *E. alphetoides*. The origin and natural hosts of *E. alphetoides* are unknown. It suddenly appeared in western Europe at the end of the nineteenth century on oaks (Mougou et al. 2008). In Switzerland, Mayor (1908) initially reported it as *Microsphaera alni* on *Q. pendunculata* (= *Q. robur*) collected in 1899 in Geneva (Beenken and Senn-Irlet 2016). At present, *E. alphetoides* has a worldwide distribution mainly on *Quercus* spp. and on other genera of the family Fagaceae. It is, however, also reported on many hosts unrelated to the Fagaceae (Braun and Cook 2012; Takamatsu et al. 2015; Table S1). Although Gadgil (2005) listed *A. altissima* as a host of *E. alphetoides* in New Zealand, ascomata were not found, and its identity was not proven by DNA sequencing. *E. picrasmae* was the only other member of *E.* sect. *Microsphaera* occurring on Simaroubaceae (Braun and Cook 2012). It has been reported on *Picrasma quassioides* from Japan, China and Korea and has very similar morphological characteristics compared to *E. alphetoides* (Braun and Cook 2012). DNA sequence data of this species is still lacking to evaluate its phylogenetic position and especially its relationship to *E. alphetoides*.

Host jumps

It is generally assumed that host jumps of plant pathogenic fungi occur mainly between closely related plant species (Bufford et al. 2016; Gilbert and Webb 2007; Gilbert et al. 2012). In contrast to this assumption, host jumps between plants of greater phylogenetic distance have been reported in powdery mildews several times (e.g., Cook et al. 2015; Kirschner 2010; Limkaisang et al. 2005, 2006; Watanabe and Sato 2009). These observed host jumps of *E. platani* and *E. alphetoides* have occurred across taxonomic boundaries

between hosts of different plant families and even orders, spilling over from Platanaceae (order Proteales) and from Fagaceae (order Fagales) to Simaroubaceae (order Sapindales), respectively. It is worth noting that *E. platani* and *E. alphitoides*, as well as both the host plants involved, *Platanus* and *Ailanthus*, are not native to Switzerland where the host jumps occurred.

In similar fashion, Kirschner (2010) reported an unusually long host jump by the North American *E. magnifica* (Sawada) U. Braun & S. Takam. from *Magnolia* (Magnoliaceae, Magnoliales) onto the Indian lotus *Nelumbo nucifera* (Nelumbaceae, Proteales) in Germany. In Japan, Watanabe and Sato (2009) found the North American *E. elevata* (Burrill) U. Braun & S. Takam, the powdery mildew of *Catalpa* (Bignoniaceae, Lamiales), on *Catharantus roseus* (Apocynaceae, Gentiales) originating from Madagascar. In both cases, neither the fungi nor the host plants were native to the location where the host jumps occurred.

Interestingly, the two oak mildews, *E. alphitoides* and the closely related *E. quercicola* S. Takam. & U. Braun, are known to infest many plant species of several families and orders all over the world (Fig. 1; Table S1 and references therein; see also Braun and Cook 2012). For example, *E. alphitoides* could be unambiguously identified by means of sequencing and infection experiments on *Wisteria* spp. (Fabaceae, Fabales) introduced as an ornamental climber from Asia to the UK (Cook et al. 2015; Denton et al. 2016). The following species also appeared within the *E. alphitoides* clade, and are morphologically very similar to *E. alphitoides*: *Erysiphe akebiae*, *E. euonymicola* U. Braun, *E. menispermi* var. *dahurica* (U. Braun & Y. Nomura) U. Braun & S. Takam., *E. orixae* (U. Braun & Tanada) U. Braun & S. Takam., *E. pseudolonicerae* (E.S. Salmon) U. Braun & S. Takam., *E. sinomenii* (Y.N. Yu) U. Braun and *E. wallrothii* (Fig. 1; Table S1; Takamatsu et al. 2015). It is, therefore, necessary to consider whether they are biologically distinct species or are conspecific with *E. alphitoides*. In the latter case, these species would be erroneously described as new to science based on misinterpretations of the undetected host jumps of *E. alphitoides* onto new plant taxa. However, it must be kept in mind that the sequences of the ITS region cannot always discriminate between biologically well-separated species (e.g., Beenken et al. 2012; Schoch et al. 2012). The *Erysiphe* sample on *Aucuba japonica* also appeared in the *E. alphitoides* clade (Fig. 1), but was distinguished by its ITS sequence and, consequently, was recently described as *E. aucubae* S. Takam. & Siahaan (Siahaan and Takamatsu 2016). Takamatsu et al. (2015) identify further clades in their phylogeny of *Erysiphe* sect. *Microsphaera*—such as the *E. aquilegiae* clade—that contain closely related mildew species that, while occurring on unrelated host plants, could not be distinguished by their ITS sequences. In contrast, some samples on the same or closely related host plants

appear in different places in the phylogeny of Takamatsu et al. (2015). Takamatsu et al. (2008) also found the host range expansion of *Phyllactinia* spp. to be independent of host plant phylogeny and discussed the implications for taxonomy and biogeography of the genus. Although polyphagous species were already known in other genera of Erysiphales—such as *Golovinomyces orontii* (Castagne) Heluta—some were revealed to be species complexes of several oligophagous species, such as the *Golovinomyces cichoracearum* complex (Braun and Cook 2012; Cunnington et al. 2010; Takamatsu et al. 2013).

In conclusion, the host range of Erysiphales appears to be not as strict as assumed in the past, especially when plants and fungi come together from biogeographically different regions and are obviously not adapted to each other. Thus, novel interactions between introduced powdery mildews and plants cannot be predicted by the evolutionary distance of the host species as recommended for phytosanitary risk analyses of biological control agents against invasive neophytes (compare Bufford et al. 2016; Gilbert and Webb 2007; Gilbert et al. 2012).

Biological control of neophytes

The tree-of-heaven is a dangerous invasive plant that must be eradicated where it invades natural habitats. Chemical control in forest stands is, however, forbidden in some countries, as is the case in Switzerland, and mechanical control entails significant effort and cost (Gurtner et al. 2015; Kowarik and Säuml 2007). Given these considerations, a biological control using pathogenic fungi could be a viable alternative (Ding et al. 2006; Kasson et al. 2014, 2015; Siegrist and Holdenrieder 2016). On the other hand, the intentional release of pathogenic fungi for biocontrol programs could also be harmful to native plants. For this reason, the introduction and release of alien organisms are strongly regulated and limited (Schaffner and Escher 2012). These regulations would not apply to *E. alphitoides* and *E. platani* because they are neomycetes that are already established in Europe (Beenken and Senn-Irlet 2016). However, both powdery mildews harm the leaves of the tree-of-heaven only weakly. The observed infections were small in size and developed late in the year at the end of the growth period. Thus, neither powdery mildew is suitable to control the neophyte. A more effective option is the *Verticillium* wilt caused by *V. nonalfalfae* Inderb. et al. that kills the tree-of-heaven (Kasson et al. 2014, 2015; Maschek and Halmschlager 2016; Siegrist and Holdenrieder 2016). This strain of *V. nonalfalfae* specific to the tree-of-heaven may be proposed as a biocontrol agent. Currently, it is only known in the USA and some locations in Austria (Kasson et al. 2014, 2015; Maschek and Halmschlager 2016; Siegrist and Holdenrieder 2016).

Conclusion

Plants appear to be protected against pathogens that are not adapted to them by a general resistance, the so-called “non-host” resistance (e.g., Antonovics et al. 2013; Gill et al. 2015; Lipka et al. 2010). In contrast, the present study, as well as the publications cited in it, show that some fungal pathogens of Erysiphales can overcome this non-host resistance of plants unrelated to their original hosts. This is particularly the case if fungi and their novel host plants had not been in contact before they came together from biogeographically different regions. In this way, the plant resistance mechanism obviously could not adapt to these novel non-host pathogens.

In summary, the observations of powdery mildews on novel hosts have the following consequences in plant pathology.

- (i) In taxonomy, undetected host jumps could result in wrong identification of species if based more or less only on the host ranges of the pathogenic fungi—which was often the case especially in the time before DNA barcoding. New taxa should be established only after verification by molecular phylogeny.
- (ii) In conservation management, the possibility of unexpected host jumps must be taken into account when assessing the risks of introducing particular fungi.
- (iii) In molecular plant pathology, more detailed investigation of cross-family and cross-order host jumps could contribute to improved understanding of fungal infection and plant resistance mechanisms.

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