Article

Fallopia ×moravica (Polygonaceae), a new hybrid between *Fallopia compacta* and *F. sachalinensis*

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Abstract

A new knotweed hybrid originating from the crossing of *Fallopia compacta* and *F. sachalinensis* is described based on plant material collected in the Moravia region in the Czech Republic as *F. ×moravica.* In addition to the Czech Republic, the hybrid has also been reported previously from the United Kingdom and New Zealand; however, it was not distinguished from *F. ×bohemica*, a hybrid between *F. japonica* and *F. sachalinensis*, since its one parent (*F. compacta*) has been generally treated only as a variety of *F. japonica*. *F. ×moravica* differs from the morphologically most similar hexaploid (2n = 6x = 66) *F. ×bohemica* by its tetraploid (2n = 4x = 44) number of chromosomes and by the constant absence of purple spots on stem internodes (which are usually present in *F. ×bohemica*). The new hybrid also differs from *F. ×bohemica* as well as other European *Fallopia* members by its unique relative genome size. Other potential morphological and cytological differences of *F. ×moravica* from the related *F. ×bohemica* are discussed.

Keywords: alien flora, Bohemian knotweed, flow cytometry, hybridisation, invasion, Moravia, *Reynoutria*

Introduction

The genus *Fallopia* Adanson (1763: 274, 277), with approximately 44 species when accepting the broad generic concept (see below), is globally known for invasive representatives classified into the section *F.* sect. *Reynoutria* (Houttuyn 1777: 639) Ronse Decr. in Ronse Decraene & Akeroyd (1988: 346), in the narrow sense into the genus *Reynoutria* Houttuyn (1777: 639). In the broader sense, to which we also lean in our work, the genus *Fallopia* is composed of five sections (Desjardins 2015): *F.* sect. *Fallopia*, *F.* sect. *Parogonum* Haraldson (1978: 78), *F.* sect. *Muehlenbeckia* (Meisner 1841a: 316, 1841b: 227; combination in the genus *Fallopia* not effectively published yet, cf. Desjardins 2015: 189), *F.* sect. *Reynoutria*, and *F.* sect. *Sarmentosae* (I.Grintz. in Guşuleac 1952: 645) Holub (1971: 176). The sections are characterised by two putative synapomorphies: the presence of nectariferous glands at the base of leaf petioles (extrafloral nectaries) and the *Tiniaria*-type pollen (Desjardins 2015). An important argument for support of the mentioned broader generic concept is the relatively frequent hybridisation between sections and, conversely, the absence of hybridisation of these sections with other closely related genera, such as *Atraphaxis* Linnaeus (1753: 333), *Duma* T.M.Schuster in Schuster *et al.* (2011: 1061), or *Polygonum* Linnaeus (1753: 359) (for details, see Bailey 2013 and Desjardins 2015).

Fallopia sect. *Reynoutria*, a group of approximately 6 species native to East Asia (Desjardins 2015), is represented by four naturalized alien species in Europe: *F. compacta* (Hooker 1880: tab. 6476) G.H.Loos & P.Keil in Loos (2010: 121; this taxon is often treated as a variety of *F. japonica*, note to its taxonomic status see below), *F. japonica* (Houttuyn 1777: 640) Ronse Decr. in Ronse Decraene & Akeroyd (1988: 369), *F. multiflora* (Thunb. in Murray

1784: 379) Haraldson (1978: 77), and *F. sachalinensis* (F.Schmidt in Maximowicz 1859: 233) Ronse Decr. in Ronse Decraene & Akeroyd (1988: 369) (Bailey 1989, Bímová *et al.* 2001, Bailey *et al.* 2007, Beringen *et al.* 2019). While *F. compacta* and *F. multiflora* are only rarely found in Europe and currently do not represent a significant threat to European ecosystems (Bailey & Wisskirchen 2006, Balant 2015, Beringen *et al.* 2019), the remaining two species (*F. japonica*, *F. sachalinensis*) are regarded as dangerous weeds that have a significant impact on reducing native plant diversity across the temperate zone of the continent (e.g., Richardson *et al.* 2000, Bímová *et al.* 2003, Moravcová *et al.* 2011, Alberternst & Böhmer 2011, Bailey 2013, Lavoie 2017).

The first species of *Fallopia* sect. *Reynoutria* imported to Europe (in 1823 or 1825) was *F. japonica* (Beerling *et al.* 1994, Bailey & Conolly 2000, Balogh 2008). In the native range of East Asia (Shimoda &Yamasaki 2016), *F. japonica* has not yet been satisfactorily resolved on taxonomy, with several varieties recognised, e.g., *F. japonica* var. *hachidyoensis* (Makino 1928: 21) Yonekura & Ohashi (1997: 158), *F. japonica* var. *uzenensis* (Honda 1932: 675) Yonekura & Ohashi (1997: 158), and others (Kim & Park 2000, Bailey 2003, Bailey *et al.* 2007, Balogh 2008, Desjardins 2015, Beringen *et al.* 2019). In contrast, in the European and North American adventive range of *F. japonica*, the species has been part of many studies, and its morphology, cytology and genetics are well understood. In those regions, only two varieties were previously recognised: the noninvasive, exclusively tetraploid, *F. japonica* var. *compacta* (Hooker 1880: tab. 6476) Bailey (1989: 443) and the extremely troublesome, invasive, mostly octo- or rarely hexaploid, *F. japonica* var. *japonica* (e.g., Bailey & Wisskirchen 2006, Bailey *et al.* 2007, Tiébré *et al.* 2007a, Suda *et al.* 2010, Duistermaat *et al.* 2012, Strgulc Krajšek & Dolenc Koce 2015, Bzdega *et al.* 2016, Clements *et al.* 2016, Gillies *et al.* 2016). Except for morphology (see below), significant differences in *F.* var. *compacta* from *F. japonica* var. *japonica* (and from other representatives of *F.* sect. *Reynoutria*) have also been demonstrated at the molecular level (Galasso *et al.* 2009, Desjardins 2015). Thus, *F. japonica* var. *compacta* was recently mostly accepted as a separate species [*F. compacta* (Hook.f.) G.H.Loos & P.Keil] by several authors (see e.g., Loos 2010, Desjardins 2015) [sometimes reported as *Reynoutria compacta* (Hook.f.) P.D.Sell in Sell & Murrell 2018: 687; see e.g., Groom 2011], which was followed in the present study (but see for example Kim & Park 2000, according to which *F. compacta* does not merit formal taxonomic recognition). In Europe, *F. japonica* is morphologically and genetically relatively uniform, and all populations can be assigned to a nominal variety, *F. japonica* var. *japonica* (Balogh 2008, Desjardins 2015, Holm *et al*. 2018).

Fallopia compacta (at least in its adventive range) and *F. japonica* var. *japonica* are quite clearly distinguishable by several morphological traits: *F. compacta* has a smaller height, only 0.3–1.3 m (1.5–4.5 m in *F. japonica* var. *japonica*), significantly purple stems and flowers, small, 4–7(–10) cm long leaves (9–19 cm in *F. japonica* var. *japonica*), which are as long as broad, with a rounded or strongly truncated base, undulate (wavy) margins, and an abruptly cuspidate apex (Hlaváček *et al.* 1996, Balogh 2008, Alberternst & Böhmer 2011, Desjardins 2015, Sell & Murrell 2018, Mandák & Pyšek 2019). In Europe, in comparison to *F. japonica* var. *japonica*, which is represented almost exclusively by (effectively/functionally) female (male sterile) individuals, *F. compacta* consists of either male sterile (functionally/effectively female) or male fertile (functionally/effectively male or hermaphrodite) individuals (Bailey *et al.* 1996, 2007, Hollingsworth *et al.* 1999). However, it should be mentioned that several cultivars sold under the species name of *F. japonica* are commercially available in Europe (Beringen *et al*. 2019), and their identities are not always clear.

In both native and adventive ranges, the representatives of *Fallopia* sect. *Reynoutria* are, apart from their invasiveness, also known for their large intraspecific ploidy variation and hybridisation. However, within mature individuals of *F.* sect. *Reynoutria*, mainly euploid cytotypes, were recorded (diploid, 2n = 2x = 22; tetraploid, 2n = 4x = 44; hexaploid, 2n = 6x = 66 and octoploid, 2n = 8x = 88; Bailey & Stace 1992, Pashley 2003, Suda *et al.* 2010, Park *et al.* 2018); in their seedlings, various aneuploid counts were confirmed, which in the vast majority of cases are unable to survive in nature and die before reaching maturity (Tiébré *et al.* 2007b, Bailey *et al.* 2009, Saad *et al.* 2011, Bailey 2013, Strgulc Krajšek & Dolenc Koce 2015). The mentioned cytological variability of knotweeds is also manifested within taxa, while other cytotypes may predominate in native and other exotic ranges. In Europe, within *F. compacta* and *F. multiflora*, only one ploidy was found (2n = 4x = 44 in *F. compacta*, 2n = 2x = 22 in *F. multiflora*), while in two other knotweed representatives, several were found: *F. japonica* var. *japonica* is mostly octo-, rarely hexaploid, and *F. sachalinensis* is mostly tetra-, rarely hexa- or octoploid (Bailey 1989, Bailey & Stace 1992, Bailey & Wisskirchen 2006, Tiébré *et al.* 2007a, Suda *et al.* 2010, Duistermaat *et al.* 2012, Bzdega *et al.* 2016, Desjardins 2015, Holm *et al*. 2018).

Within the genus *Fallopia*, the hybrids can originate by both inter- and intrasectional hybridisation (Bailey & Stace 1992, Bailey 2013, Desjardins 2015). Among the intersectional hybrids, the best-known is *F. ×conollyana* Bailey (2001: 539), a hybrid between diploid *F. baldschuanica* (Regel 1884: 684) Holub (1971: 176) (member of *F.* sect.

Sarmentosae) and octoploid *F. japonica* var. *japonica* (member of *F*. sect. *Reynoutria*) (e.g., Bailey 1988, 2001, 2013, Stace & Crawley 2015, Keil & Fuchs 2019). Within *F*. sect. *Reynoutria*, the most well-known hybrid is *F. ×bohemica* (Chrtek & Chrtková 1983: 120) Bailey (1989: 443), a hybrid between *F. japonica* and *F. sachalinensis* (the type specimen of *F. ×bohemica* represents the hybrid between *F. japonica* var. *japonica* and *F. sachalinensis*). The hybrid was described from the Czech Republic from the vicinity of the Běloves spa near the town of Náchod ("prope balneas Běloves, non procul ab opp. Náchod", currently part of the Náchod town; Chrtek & Chrtková 1983, as *Reynoutria ×bohemica* Chrtek & Chrtková). The hybrid, of which all European populations probably arose in Europe (Desjardins 2015), attracts considerable attention mainly due to its extreme invasiveness, which is even higher than those of the parental species (e.g., Bímová *et al.* 2001, 2003, Pyšek *et al.* 2003, Moravcová *et al.* 2011, Bailey 2013, Gillies *et al.* 2016).

Detailed cytotype screening of mature European *Fallopia ×bohemica* individuals revealed three major cytotypes: tetra-, hexa- and octoploid, with the hexaploid cytotype clearly predominant (Mandák *et al.* 2003, Bailey & Wisskirchen 2006, Tiébré *et al.* 2007a, Suda *et al.* 2010, Holm *et al.* 2018, Desjardins *et al*. 2022). It is well documented that the hexaploid cytotype originated from the unidirectional crossing between female octoploid *F. japonica* var. *japonica* and functionally male tetraploid *F. sachalinensis* (Bailey & Wisskirchen 2006, Hollingsworth *et al*. 1999, Desjardins *et al*. 2022). In contrast, the octoploid cytotype of *F. ×bohemica* may have several theoretical routes of origin (e.g., pollination of female octoploid *F. japonica* var. *japonica* by an unreduced gamete from functionally male tetraploid *F. sachalinensis*), but none has yet been proven with certainty (Bailey & Wisskirchen 2006, Bailey *et al.* 2007, Bailey 2013, Desjardins *et al*. 2022). Thus, the taxonomy of octoploid *F. ×bohemica* requires further study.

The tetraploid *Fallopia ×bohemica* was first revealed in the 1980s in England (the United Kingdom; e.g., Bailey & Conolly 1985, as "*Reynoutria* tetraploids", Bailey 1989 as "4x Hybrid *Reynoutria*", Bailey *et al.* 1996 and 2007 as "tetraploid *F. ×bohemica*") and later in the Moravia region in the eastern part of the Czech Republic (Olomouc town and Račice village; Mandák *et al.* 2003 as "tetraploid *Reynoutria ×bohemica*"; Fig. 1). Most recently, the tetraploid hybrid cytotype was found in New Zealand (Desjardins 2015: 156, 158, Desjardins *et al*. 2022). It is considered by all authors that tetraploid *F. ×bohemica* is the result of bidirectional hybridisation between tetraploid *F. compacta* (reported in previous studies usually as *F. japonica* var. *compacta*) and tetraploid *F. sachalinensis* (e.g., Bailey *et al.* 1996, Mandák *et al.* 2003, Bailey & Wisskirchen 2006, Tiébré *et al.* 2007a, Bailey 2013, Stace & Crawley 2015). This fact was also confirmed in English and New Zealand plants by molecular data (Hollingsworth *et al.* 1999, Pashley 2003, Tiébré *et al.* 2007a, Desjardins 2015, Desjardins *et al*. 2022). In the case of Moravian plants, isozyme data also point to their origin from hybridisation between *F. compacta* and *F. sachalinensis* (Mandák *et al*. 2005: 224).

If *Fallopia compacta* is accepted at the species level (see above), the name *F. ×bohemica* can be used only for individuals originating from the crossing of *F. japonica* and *F. sachalinensis*. Therefore, it is necessary to find a new name for the descendants of the hybridisation of *F. compacta* and *F. sachalinensis*, which has not been done thus far. Based on these facts, we describe the descendants of a crossing between *F. compacta* and *F. sachalinensis*, collected in the Moravia region, as a new hybrid, named *F. ×moravica*.

Moravian plants of *Fallopia ×moravica* have so far only been cytologically analysed by flow cytometry (Mandák *et al.* 2003, Suda *et al*. 2010) and no one has counted the exact number of their chromosomes. Moreover, to our knowledge, no one has yet investigated the ploidy level of the type specimen of *Fallopia ×bohemica*, nor the individuals at its type locality [the closest cytologically analysed populations of *F. ×bohemica* are located from its type locality at distances of approximately 34 km (Vamperk town) and 57 km (Poniklá village), respectively; cf. Mandák *et al.* 2003]. Therefore, the aim of our study was to clarify this question as well.

Material and methods

Plant material
For cytological analyses and morphological research, we collected plant material of *Fallopia ×moravica* from 12 sites in Moravia (altogether 31 stands; Fig. 1), and plant material of *F. ×bohemica* from the area from which the hybrid was described (altogether 17 stands from 8 sites) collected near former Běloves spa in Náchod town; Fig. 2) during 2021 and 2022 (all in the Czech Republic; Table 1). Voucher specimens are stored in the SAV herbarium. A stand (as well as an individual) is defined here as a compact colony of knotweed shoots in one locality, with at least 3 m distance from other such colonies. In our analyses, each stand (individual) was usually represented by one shoot.

Pop. no.	Locality description	Coordinates	Stand no.	2C genome size (a. u.)	FCM analyses
F. ×moravica					
495[T]	CZ, Moravia, Olomouc-Černovír borough, left embankment of the Morava river, alluvial meadow and mowed grassland, 208 m, 1 October 2021, IH; 27 June 2022, IH & PM	49°36′24″ N 17°15′26″ E	495-1[(*)T]	1.217–1.227; 2n = 44	2
			495-2*	1.217–1.224	2
			495-3*	1.224	1
496[1]	CZ, Moravia, Olomouc-centre, on the corner of Na Letné and Václava III streets, mowed grassland, 208 m, 1 October 2021, IH; 27 June 2022, IH & PM (several small stands on site)	49°36′06″ N 17°15′52″ E	496-1*	1.223	1
			496-2*	1.220	1
497[1]	CZ, Moravia, Olomouc-centre, Na Letné street, right embankment of the Morava river, alluvial meadow and mowed grassland, 206 m, 1 October 2021, IH; 27 June 2022, IH & PM	49°36′00″ N 17°15′57″ E	497-1*	1.214–1.233	2
1073	CZ, Moravia, Olomouc-Lazce borough, on the corner of Černochova and Václava III streets, cultivated in garden, 208 m, 27 June 2022, IH & PM	49°35′59″ N 17°15′40″ E	1073	1.214	1
1074	CZ, Moravia, Olomouc-centre, on the corner of Dlouhá and Václava III streets, left bank of the Mlýnský potok stream, alluvial meadow, mowed grassland and edge of floodplain forest, 209 m, 27 June 2022, IH & PM; 1 July 2022, PM; 24 August 2022, PM	49°35′56″ N 17°15′36″ E	1074-1	1.220	1
			1074-2	1.210	1
			1074-3	1.228	1
			1074-4*	–	–
			1074-5*	–	–
			1074-6*	–	–
			1074-7	1.224	1
			1074-8*	–	–
			1074-9*	–	–
			1074-10*	1.231	1
			1074-11*	1.231	1
1075[1]	CZ, Moravia, Olomouc-centre, Na Letné street, right embankment of the Morava river, alluvial meadow and mowed grassland, 207 m, 27 June 2022, IH & PM; 24 August 2022, PM	49°36′03″ N 17°15′56″ E	1075-1*	1.223	1
			1075-2*	1.233	1
1077	CZ, Moravia, Olomouc-Černovír borough, left embankment of the Morava river, mowed grassland, 209 m, 1 July 2022, PM	49°36′33″ N 17°15′25″ E	1077*	1.220	1
1081	CZ, Moravia, Olomouc-Hodolany borough, on the corner of Bystrovanská and Lermontovova streets, mowed grassland, 212 m, 1 July 2022, PM; 24 August 2022, PM	49°35′48″ N 17°17′13″ E	1081-1	1.221	1
			1081-2	1.218	1
			1081-3*	1.212	1
			1081-4	1.228	1

TABLE 1 (1/2). (Continued)

Pop. no.	Locality description	Coordinates	Stand no.	2C genome size (a. u.)	FCM analyses
1083[2]	CZ, Moravia, Račice-Pístovice, Račice castle, north-east foot of the castle walls, forest, 396 m, 1 July 2022, PM	49°16′33″ N 16°52′07″ E	1083-1*	1.211–1.214	2
			1083-2	1.216	1
			1083-3	1.222	1
1193	CZ, Moravia, Olomouc-Hodolany borough, on the edge of the bicycle path on the left embankment of the Bystřice stream, 210 m, 24 August 2022, PM	49°35′49″ N 17°17′09″ E	1093*	1.235	1
1197	CZ, Moravia, Olomouc-Holice borough, 650 m north–north–west from the Nový Dvůr settlement, mowed grassland and cultivated trees along a road, 213 m, 24 August 2022, PM	49°33′17″ N 17°16′26″ E	1197	1.225	1
1199	CZ, Moravia, Olomouc-Holice borough, 780 m west from the southern edge of the Nový Dvůr settlement, left bank of the Morava river, waste grounds on the edge of floodplain forest, 217 m, 24 August 2022, PM	49°32′36″ N 17°16′10″ E	1199-1	1.225	1
			1199-2	1.221	1
F. ×bohemica					
1181	CZ, Bohemia, Náchod town, former spa of Běloves, Promenádní street, north-east part of the spa park and left embankment of the Metuje river, 346 m, 23 August 2022, PM	50°25′12″ N 16°11′28″ E	1181-1*	1.850	1
			1181-2(*)	1.859	1
			1181-3*	1.867	1
			1181-4	1.863	1
1182	CZ, Bohemia, Náchod town, former spa of Běloves, central part of the spa park, 346 m, 23 August 2022, PM	50°25′10″ N 16°11′28″ E	1182-1*	1.855	1
			1182-2*	1.852	1
1183	CZ, Bohemia, Náchod town, former spa of Běloves, east part of the spa park, 346 m, 23 August 2022, PM	50°25′10″ N 16°11′32″ E	1183(*)	1.860	1
1184	CZ, Bohemia, Náchod town, former spa of Běloves, end of the Lázeňská street, cultivated and growing in the wild along the road, 355 m, 23 August 2022, PM	50°25′08″ N 16°11′27″ E	1184-1*	1.863	1
			1184-2*	1.863	1
			1184-3*	1.864	1
			1184-4	1.863	1
			1184-5*	1.863	1
1185	CZ, Bohemia, Náchod town, former spa of Běloves, U Lomu street, waste grounds along the forest road, 356 m, 23 August 2022, PM	50°25′08″ N 16°11′32″ E	1185*	1.854	1
1186	CZ, Bohemia, Náchod town, Běloves, U Lomu street, waste grounds along the forest road, 364 m, 23 August 2022, PM	50°25′09″ N 16°11′38″ E	1186*	1.868	1
1187	CZ, Bohemia, Náchod town, Běloves, edge of the forest road before entering the (former) Kačerů lom stone quarry, 380 m, 23 August 2022, PM	50°25′08″ N 16°11′48″ E	1187	1.857	1
1188	CZ, Bohemia, Náchod town, Běloves, (former) Kačerů lom stone quarry, edge of a forest and along the water of the flooded quarry, 385 m, 23 August 2022, PM	50°25′08″ N 16°11′49″ E	1188-1	1.872	1
			1188-2	1.867	1

1   *Fallopia ×moravica* was from the same or close locality already published in Mandák *et al.* [2003, sub "*Reynoutria ×bohemica* (2n = 44)"] and Suda *et al.* [2010, sub "*Fallopia ×bohemica* (2n = 44)"]: "Olomouc, on both banks of the Morava river, near the Institute of Experimental Botany, 49°36′09.11″ N, 17°15′54.92″ E, coll. B. Mandák et P. Pyšek, 12. 6. 1998, pop. no. 28".

2   *Fallopia ×moravica* was from the same or close locality already published in Mandák *et al.* [2003, sub "*Reynoutria ×bohemica* (2n = 44)"] and Suda *et al.* [2010, sub "*Fallopia ×bohemica* (2n = 44)"]: "Račice (Vyškov), in the castle campus, 49°16′33.42″ N, 16°52′03.31″ E, coll. B. Mandák et P. Pyšek, 16. 6. 1998, pop. no. 25".

FIGURE 1. A. Distribution of *Fallopia ×moravica* in the Czech Republic (blue squares) and location of the type locality of *F. ×bohemica* in Náchod town, Běloves spa (pink square). – **B., C., D., E., F., G.** Detailed location of analysed *F. ×moravica* stands in Olomouc town and Račice village. The type locality of *F. ×moravica* is marked with a yellow arrow. The stand numbers follow those in Table 1. Map backgrounds: mapy.cz (B) and earth.google.com (C–G).

We did not analyse the ploidy level of the type specimen of *F. ×bohemica* (deposited in PR), as in our previous research, we were unable to analyse herbarium specimens of *F.* sect. *Reynoutria* members by flow cytometry (Mereďa Jr., ined.).

Chromosome counting

For chromosome counting, one (the type) individual of *Fallopia ×moravica* was collected in Moravia (Table 1). After digging, the washed parts of the rhizomes were left for 1 week at a temperature of 22 °C in a plastic bag for rooting. Subsequently, root tip meristems from this plant were employed. The root tips were pretreated in a 0.002 M water solution of 8-hydroxyquinoline at 4 °C for approximately 16 h (overnight), fixed in a 1:3 mixture of 98% acetic acid and 96% ethanol for 1–24 h, washed in distilled water, macerated in 1 N HCl at 60 °C for 9 min and washed in distilled water again. Tip squashes were made using the cellophane square technique (Murín 1960). Permanent slides were stained with a 7% solution of Giemsa Stain – Modified Solution (Fluka Analytical) in Sörensen phosphate buffer, dried

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and observed in a drop of immersion oil using a Leica DM 1000 microscope equipped with an HDCE-X5 camera, and ScopeImage 9.0 software was used for observation of chromosomes.
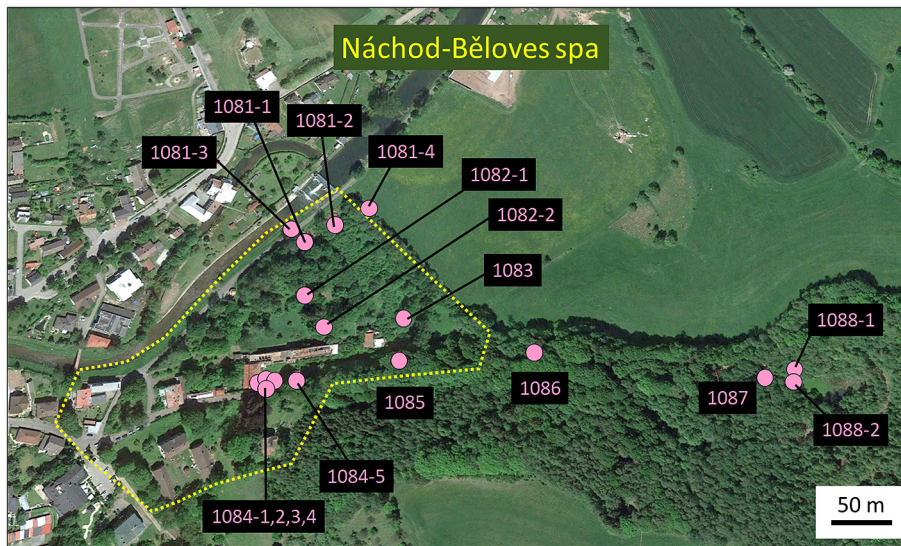

FIGURE 2. Location of analysed *Fallopia ×bohemica* stands at the type locality in Náchod town, in the former Běloves spa and surroundings. The yellow dashed line delimits the approximate area of the former spa. The stand numbers follow those in Table 1 (in 2022, there were no other knotweed stands occurring in the displayed area). Map background: earth.google.com.
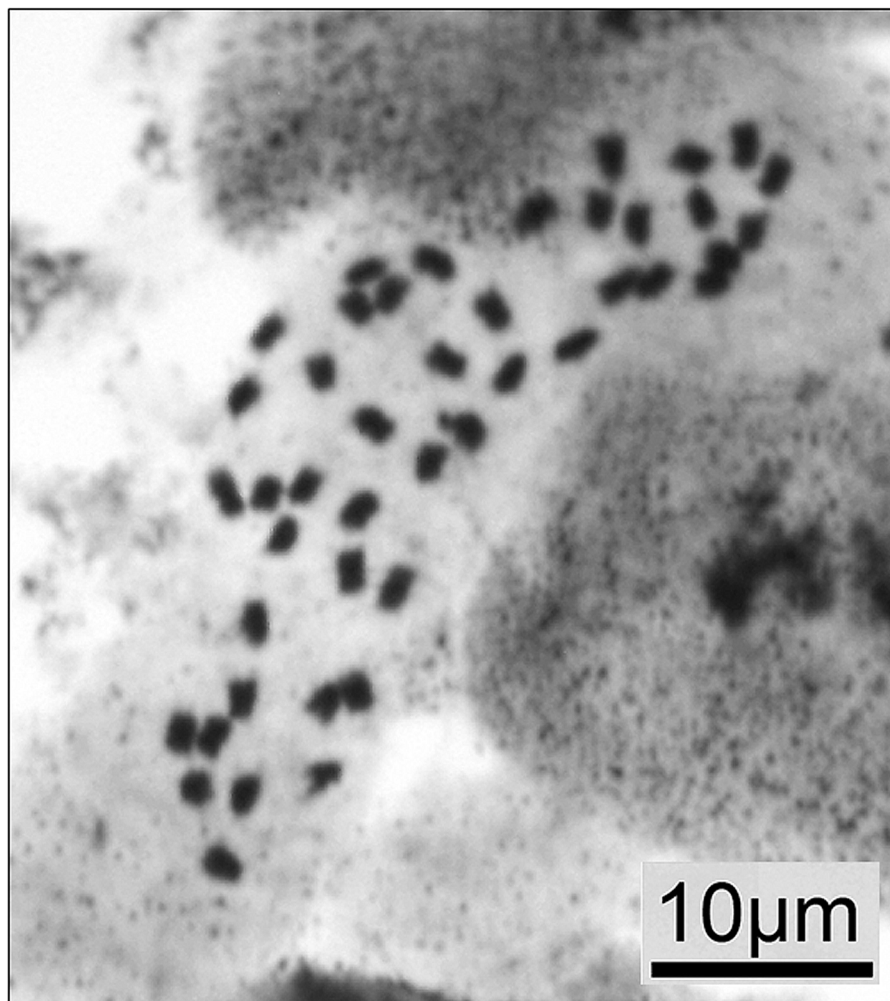
FIGURE 3. Metaphase plate of a root tip of *Fallopia ×moravica* with chromosome number 2n = 44 (stand no. 495-1). Photo by Mártonfiová, L.

Flow cytometry

The DNA ploidy levels and relative genome sizes (further RGS) of 31 *Fallopia ×moravica* and 17 *F. ×bohemica* stands [each represented usually by one (rarely two) shoot(s); see Table 1] collected from 12 and 8 sites, respectively, in the Czech Republic (Figs. 1 & 2) were determined using flow cytometry (FCM). The obtained data were compared with RGS data of *Fallopia* taxa collected throughout Central Europe as part of another study (Mereďa *et al.*, in prep.). Among the representatives of the *Fallopia* genus reported from Central Europe, we failed to record only the species *F. compacta* (see Discussion); we took the data for this species from the work of Suda *et al.* (2010).

Only fresh leaves collected in the field and stored for up to 5 days at 4–10 °C in plastic bags with a small amount of water were used. Fresh material was favoured over silica-gel-dried samples because, in our experience, FCM using fresh material provides more accurate results than those using desiccated tissues (cf. Mereďa *et al.* 2019b). RGS expressed in relative fluorescence intensities of a sample compared to the standard were estimated by flow cytometry at the Institute of Botany Plant Science and Biodiversity Centre, Slovak Academy of Sciences in Bratislava. The relationship between RGS and ploidy level was established using reference plants with known chromosome counts obtained from *Fallopia ×moravica* (Fig. 3, this study), *F. ×bohemica* (2n = 66), *F. sachalinensis* (2n = 44, 66), and *F. japonica* (2n = 88) individuals (all Mereďa *et al.*, in prep.) with known chromosome numbers. The symbol "~" means "approximately" and is used in text when the referenced ploidy level corresponds not only to the euploid chromosome number but also to the derived aneuploid number(s) of chromosomes. The sample preparation and FCM procedure followed that of Mereďa *et al.* (2019a). As an internal reference standard, *Bellis perennis* L. ($2C = 3.38$ pg; Schönswetter *et al.* 2007) was used in all analyses. The RGS (relative $2C$ value) of each sample was calculated as the mean of the $G0/G1$ peak of the fluorescence intensity of the sample divided by the mean of the $G0/G1$ peak of the fluorescence intensity of the standard. The monoploid RGS (relative $1Cx$ value) corresponds to the RGS of the nonreplicated monoploid genome with number x. The monoploid RGS was calculated as the relative $2C$ DNA value divided by the number of chromosome sets x (Greilhuber *et al.* 2005). The RGS is given in arbitrary units relative to the standard used (a. u.). To ensure the accuracy of RGS estimations, each plant was analysed separately, and only those histograms were considered in which both *Fallopia* and standard G0/G1 peaks were symmetrical and similar in height, and the coefficient of variation (CV) was below 3.5%.

Results and discussion

Chromosome counting of F. ×moravica

A direct count gave 2n = 44 for a *Fallopia* plant from population no. 495, ind. no. 1 (Fig. 3, Table 1).

Flow cytometry of F. ×moravica and F. ×bohemica

DAPI staining yielded high-resolution histograms with little background noise and low CVs (Fig. 4). The mean CVs of standard and *Fallopia* samples were 2.66% and 2.44%, respectively. The RGS values of *F. ×moravica* samples ranged between 1.210 and 1.235 a. u. (mean 1.222 a. u., standard deviation 0.007), those of *F. ×bohemica* samples from the vicinity of Běloves spa (the type locality of the hybrid) ranged between 1.850 and 1.872 a. u. (mean 1.861 a. u., standard deviation 0.006). The intraspecific RGS variation was very small in both nothotaxa (2.0 and 1.2%, respectively; see Tables 1 and 2). The RGS values of *F. ×moravica* plants showed that all individuals are tetraploid (2n = 4x ~ 44), while all analysed plants of *F. ×bohemica* from the type locality are hexaploid (2n = 6x ~ 66). The values of *F. ×bohemica* from the type locality were identical to the values of hexaploid individuals of *F. ×bohemica* from other Central European localities (Table 2). *Fallopia ×moravica* differed in RGS values from all other taxa occurring in Central Europe, being intermediate between the values of the parental species (Table 2).

Taxonomy

Fallopia ×moravica Hodálová & Mereďa Jr., *hybr. nov.* (= *Fallopia compacta* × *F. sachalinensis*).

Holotype:—CZECH REPUBLIC. Moravia, Olomouc-Černovír borough, left bank of the Morava River, alluvium (Fig. 5), Lat. 49°36′24″N; Long. 17°15′26″E, elev. 208 m., 27 June 2022, Hodálová, I. & Mereďa, P. Jr., population no. 495, ind. no. 1 (SAV0013900!, barcode SAV0013900, Fig. 6).

Diagnosis:—*Fallopia ×moravica* is a hybrid between *F. compacta* and *F. sachalinensis*. It differs from the morphologically most similar *Fallopia* hybrid *F. ×bohemica* [= *F. japonica* × *F. sachalinensis*] by its tetraploid DNA

level (2n = 4x ~ 44), smaller relative genome size (1.210–1.235 a. u.) and consistently green stems, without purple spots around the bumps. *Fallopia ×moravica* differs from *F. compacta* by its higher stems, larger leaves and slightly to deeply cordate lamina leaf base; from *F. sachalinensis,* it differs by its smaller leaves and smaller trichomes on the lower leaf surface (see Description). The relative genome size also reliably differentiates *F. ×moravica* from both parental species as well as from all other *Fallopia* representatives occurring in Central Europe.

TABLE 2. 2*C* relative and 1*Cx* relative (monoploid) genome sizes (in arbitrary units; a. u.) of mature individuals of the Central European representatives of the genus *Fallopia* (arranged according to their mean 2*C* RGS). N_S/N_P number of stands (individuals)/populations analysed. As an internal reference standard, *Bellis perennis* (2*C* = 3.38 pg) was used in all analyses.

Taxon (DNA ploidy level)	Relative genome size (a. u.)			Reference
	N_S/N_P	2*C* (holoploid) min.–max.	1 *Cx* (monoploid) min.–max.	
F. dumetorum (Linnaeus 1762: 521) Holub (1971: 176) (2*n* = 2*x* ~ 20)	33/13	0.40–0.42	0.20–0.21	Mereďa *et al.*, in prep.
F. complexa (Cunningham 1838: 455) J.M. Tison in Tison *et. al.* (2021: 224)[3] (2*n* = 2*x* ~ 20)	3/2	0.46–0.47	0.23–0.24	Mereďa *et al.*, in prep.
F. convolvulus (Linnaeus 1753: 364) Á.Löve (1970: 300) (2*n* = 4*x* ~ 40)	24/12	0.75–0.79	0.19–0.20	Mereďa *et al.*, in prep.
F. baldschuanica (2*n* = 2*x* ~ 20)	11/9	0.82–0.84	0.41–0.42	Mereďa *et al.*, in prep.
F. sachalinensis (2*n* = 4*x* ~ 44)	46/41	1.14–1.17	0.29–0.30	Mereďa *et al.*, in prep.
F. ×moravica **(2*n* = 4*x* ~ 44)**	**31/12**	**1.210–1.235**	**0.30–0.31**	**this study**
F. compacta (2*n* = 4*x* ~ 44)	3/3	ca 1.29–1.31[4]	ca 0.32–0.33[4]	Suda *et al.* (2010)
F. sachalinensis (2*n* = 6*x* ~ 66)	9/8	1.72–1.75	0.29–0.30	Mereďa *et al.*, in prep.
F. ×bohemica **(2*n* = 6*x* ~ 66)** **from the type locality**	**17/8**	**1.850–1.872**	**0.31**	**this study**
F. ×bohemica (2*n* = 6*x* ~ 66) from another Central European regions	775/685	1.83–1.92(–1.97)	0.31–0.32 (–0.33)	Mereďa *et al.*, in prep.
F. sachalinensis (2*n* = 8*x* ~ 88)	8/8	2.35–2.37	0.29–0.30	Mereďa *et al.*, in prep.
F. ×bohemica (2*n* = 8*x* ~ 88)	4/4	2.41–2.53	0.30–0.32	Mereďa *et al.*, in prep.
F. japonica var. *japonica* (2*n* = 8*x* ~ 88)	287/276	2.54–2.63	0.32–0.33	Mereďa *et al.*, in prep.
F. ×bohemica (2*n* = 10*x* = 107)	1/1	3.11	0.31	Mereďa *et al.*, in prep.

3   In Central Europe, the species is only cultivated.

4   Relative genome size in Suda *et al.* (2010) is reported with an internal reference standard *Glycine max* 'Polanka' (2*C* = 2.5 pg). Here, we present the expected values of the relative genome size using the standard *Bellis perennis* (2*C* = 3.38 pg).
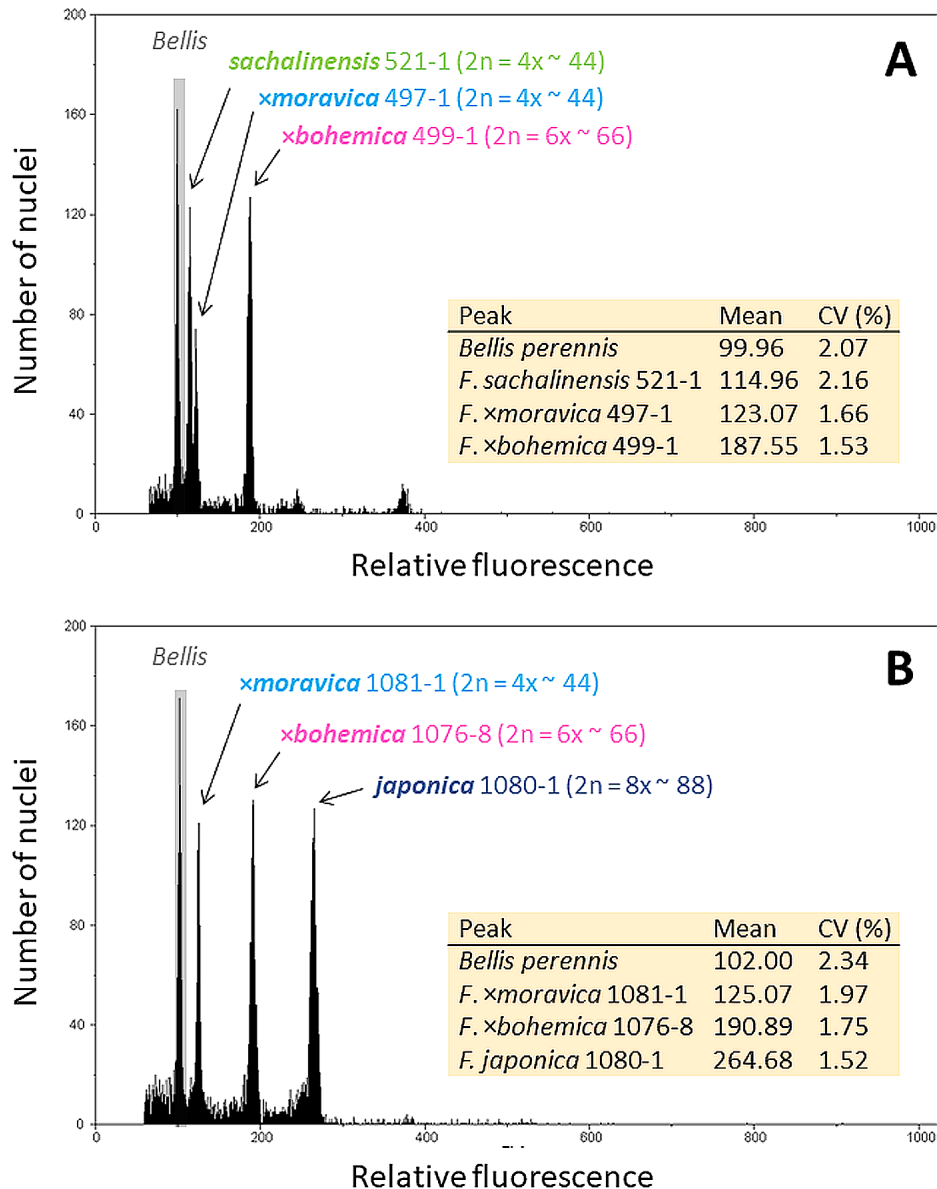
FIGURE 4. Histograms of fluorescence intensity in simultaneous analyses of DAPI-stained nuclei isolated from several *Fallopia* individuals demonstrating differences in genome sizes among *F. ×moravica* and related taxa; reference standard: *Bellis perennis* L. Combined numbers following species names denote individual plant numbers within populations. *Mean* mean peak position, *CV* coefficient of variation. Detailed information on the *F. ×bohemica*, *F. japonica* var. *japonica* and *F. sachalinensis* individuals is given in Mereďa *et al.*, in prep.

Description:—Plant intermediate between *Fallopia compacta* and *F. sachalinensis*. Gynodioecious, perennial herb with rhizomes, forming large polycormons (Fig. 7A), stems 200–350(–400) cm high, pale green, unspotted (Figs. 8A & 8B), sometimes (especially on the upper dazzled side) purplish to purple. Leaves alternate, petiole purplish or pale green, lamina of leaves from the middle part of the stem (15.3–)16.6–22.2(–24.5) cm long, (13.1–)14.4–21.4(–23.6) cm wide, broadly ovate to elliptical-ovate, at the base usually slightly cordate, rarely deeply cordate [lamina sinus depth reaching (2.1–)3.6–9.8(–16) % of lamina length], slightly to very undulate (wavy) on the margins, shortly acute at the apex, undersides often purple on the basal veins (Fig. 9); the longest hairs on the lower leaf surface (1–)2–4-cellular, (0.15–)0.2–0.35(−0.55) mm long (Fig. 10).

Etymology:—The epithet "*moravica*" refers to the geographical region of Moravia in the eastern part of the Czech Republic, where the type locality is situated.

Chromosome number:—2*n* = 4x = 44 (Fig. 3).

Relative genome size:—1.210–1.235 a. u. [in DAPI FCM using *Bellis perennis* Linnaeus (1753: 886) with 2*C* = 3.38 pg as a standard; Table 1].

Phenology:—Flowering from August to October.

FIGURE 5. Type locality of *Fallopia ×moravica* with the type individual (stand no. 495-1) in Olomouc-Černovír borough on the left bank of the Morava River and the adjacent embankment (Czech Republic). The type population consists of three separate stands; in 2022, most of these were mowed. The stand numbers follow those in Table 1. Photo by Mereďa, P. Jr., 27 June 2022.
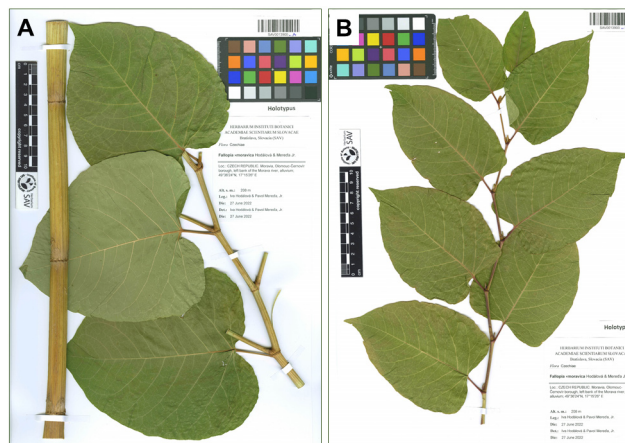

FIGURE 6. The holotype specimen of *Fallopia ×moravica* mounted on two herbarium sheets deposited in the SAV herbarium. – **A.** SAV0013900A. – **B.** SAV0013900B.

Distribution:—The Czech Republic (Moravia; Fig. 1, Table 1), the United Kingdom (England), New Zealand (the South Island).

Ecology:—The ecological demands of this taxon are almost identical to those of other members of the section *Fallopia* sect. *Reynoutria*: riverbanks, wet alluvial meadows, alluvial forests, mesophilic grasslands, roadsides, waste grounds, recultivated soils, colline and submontane deciduous forests, and cultivated plants in gardens. The occurrence of the hybrid can also be expected in other disturbed or man-made habitats from the lowlands to the mountain level (e.g., parks and sites along railways).

Invasiveness:—Considerable invasive potential.

Morphological comparison between *Fallopia ×moravica* and *F. ×bohemica*:—Among the representatives of *F.* sect. *Reynoutria*, *F. ×moravica* is the most similar to *F. ×bohemica*. Both hybrids are almost identical in height, with the same size and shape of the leaves as well as type of indumentum, which are important diagnostic morphological characters in *F.* sect. *Reynoutria* (cf. Mereďa *et al.* 2019a). It also seems that both hybrids are represented in Central Europe mostly by male fertile individuals with identical inflorescence structure (Fig. 7B). The morphological similarity between *F. ×moravica* (sub *F. japonica* var. *compacta* × *F. sachalinensis* or "tetraploid *F. ×bohemica*", respectively, in the cited studies) and *F. ×bohemica* was already highlighted by Bailey & Stace (1992: 36) and Bailey *et al.* (1996). These authors wrote that despite access to artificially resynthetized *F. ×moravica* (which was created in 1982; see

Bailey & Wisskirchen 2006: 176), they were "unable to distinguish both hybrids using any character other than chromosome number" (Bailey *et al.* 1996: 188). Several other authors (e.g., Pashley 2003, Bailey & Wisskirchen 2006, Sell & Murrell 2018: 507) made a similar statement. Only Hollingsworth *et al.* (1999: 147) note that *F. ×moravica* (reported as *F. japonica* var. *compacta × F. sachalinensis*) has in comparison to *F. ×bohemica* (reported as *F. japonica* var. *japonica × F. sachalinensis*) leaves "sometimes with undulate margins".
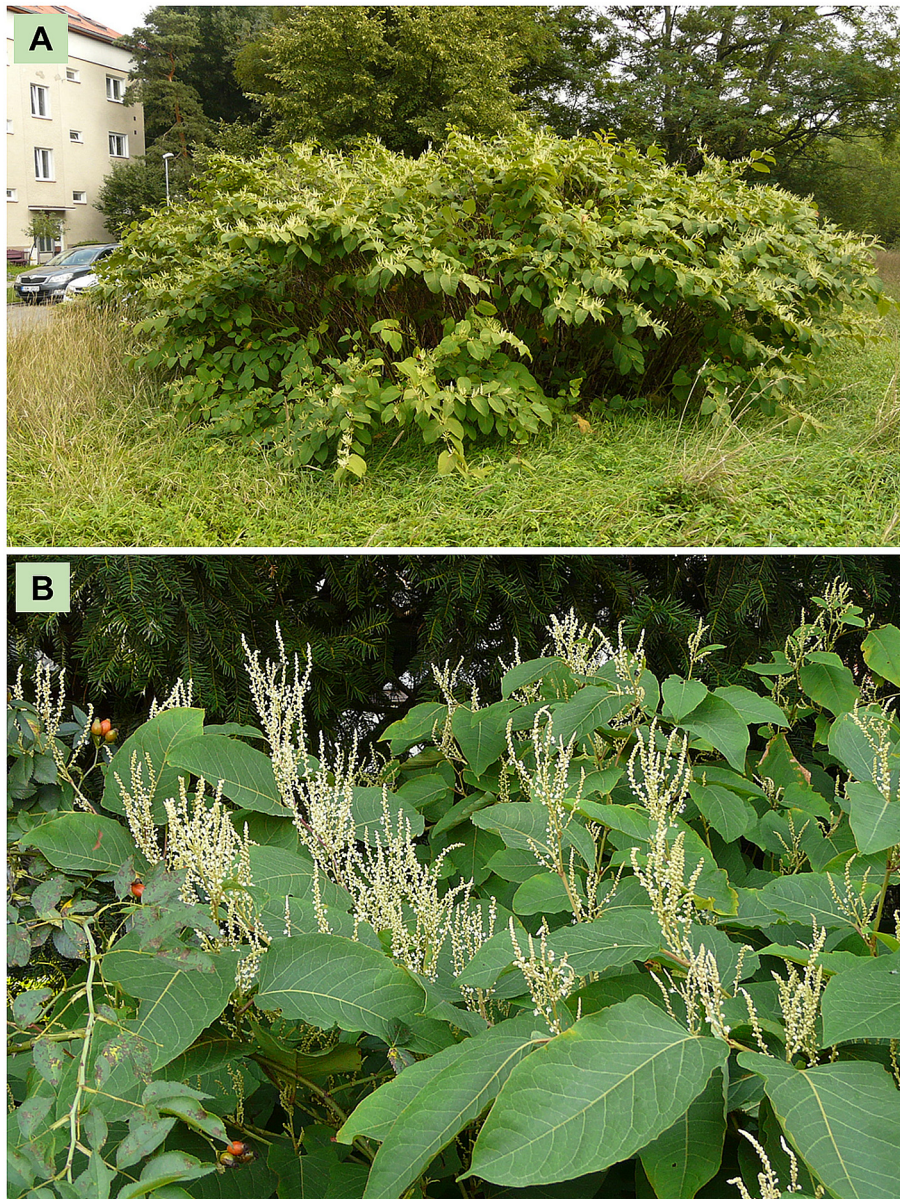

FIGURE 7. A. Mature *Fallopia ×moravica* stand (no. 1081-1) in Olomouc town (Czech Republic). – **B.** Male-fertile inflorescences of *F. ×moravica* (stand no. 1073) with characteristic very long branches, oriented strictly upright. The stand numbers follow those in Table 1. Photos by Mereďa, P. Jr., 24 August 2022.

According to our results, *Fallopia ×moravica* can be morphologically distinguished from *F. ×bohemica* at least in one trait: the constant absence of purple spots on stem internodes (Figs. 8A & 8B). In the literature, stem spotting is not mentioned anywhere when describing hybrid plants between *F. compacta* and *F. sachalinensis* (i.e., *F. ×moravica* in our study; see, e.g., Bailey *et al.* 1996, Hollingsworth *et al.* 1999, Pashley 2003, Bailey & Wisskirchen 2006, Sell & Murrell 2018, Desjardins *et al.* 2022). However, according to our research, *F. ×bohemica* typically has more or less distinct purple spots on most or at least one internode of the main stem and/or lateral branches (Figs. 8C, 8D & 8E; Stalažs 2022). In some cases, these spots on the *F. ×bohemica* plants are more difficult to identify, as they are not very prominent and could be present only on one internode within a polycormone or only on lateral young branches. The clearly spotted morphotype occurs in at least 90% of *F. ×bohemica* individuals in Central Europe, and this morphotype is also exclusively present at the type locality of the hybrid in the vicinity of Běloves spa (altogether 17 analysed

stands in 2022; Figs. 8C, 8D & 8E). *Fallopia ×bohemica* is only rarely without purple spots, and the whole stem is similar to that of *F. ×moravica*, pale green, or some parts of the stem (especially those on the upper dazzled surface) are continuously purple. Whether *F. ×moravica* inherited the spotless stem only from *F. sachalinensis* or from both parents is not currently clear. *Fallopia sachalinensis* never produces purple spots. However, we have not yet had the opportunity to observe *F. compacta*, and in the literature, stem spotting in this species is almost nowhere explicitly mentioned (e.g., Sell & Murrell 2018: 507). We found only one note on this trait in Hlaváček *et al.* (1996), who reported that this taxon has a "sparse red dotted stem". This could indicate that *F. compacta* differs from *F. japonica* var. *japonica* in this feature as well, since the stem of *F. japonica* var. *japonica* is always densely purple spotted. Although the purple spots among the Central European representatives of *F.* sect. *Reynoutria* are most prominent in *F. japonica* var. *japonica*, less prominent but are still clearly visible in most individuals of *F. ×bohemica*.
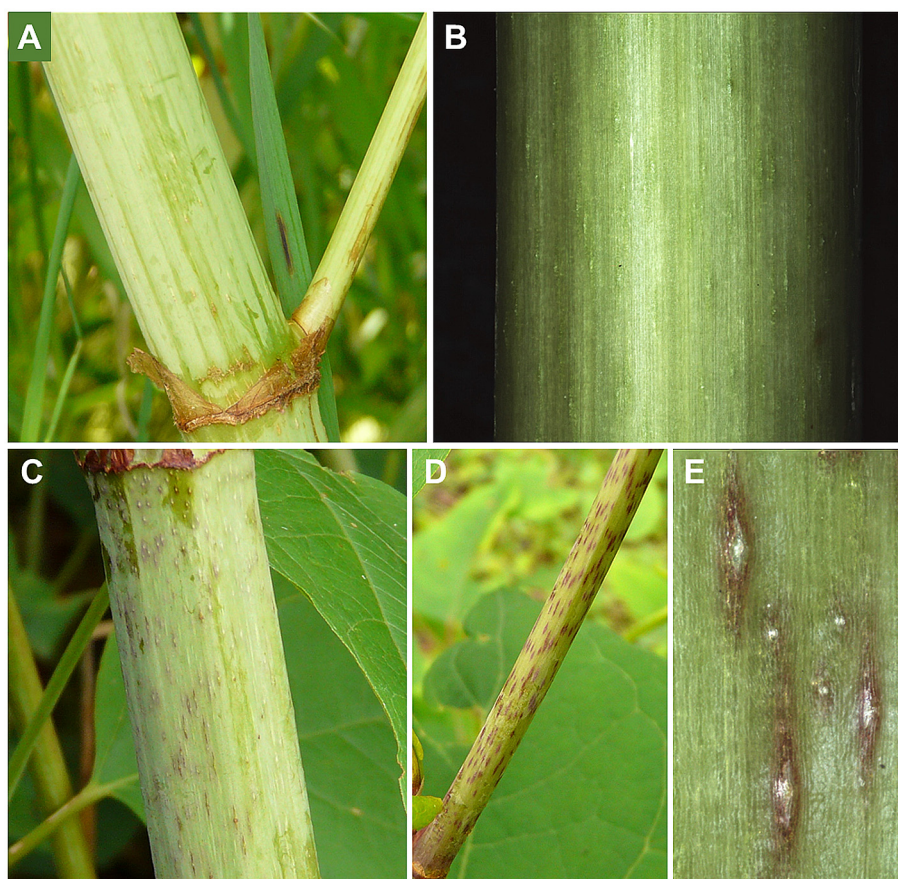

FIGURE 8. The difference in stem spotting between *Fallopia ×moravica* and hexaploid *F. ×bohemica*. – **A., B.** Internodes of the main stem (A, B) and a lateral branch (A, right side) of *Fallopia ×moravica* without purple spots (stand no. 495-1 from the type population). – **C., D., E.** The main stem (C, E) and a lateral young branch (D) of hexaploid *F. ×bohemica* with purple spots around the bumps (stand no. 1081-2 from the type population). Photos by Mereďa, P. Jr.

Both *Fallopia ×moravica* and *F. ×bohemica* are hybrids between species with very short (in *F. compacta* and *F. japonica* var. *japonica*) and very long (*F. sachalinensis*) trichomes (see Pashley 2003, Mereďa *et al.* 2019). Nevertheless, Bailey *et al.* (1996) considered that trichome characters might be useful for distinguishing tetraploid *F. ×bohemica* (i.e., *F. ×moravica* in our study) and hexaploid *F. ×bohemica* because of the different proportions of parental genomes in these two hybrids (1:1 in tetraploid *F. ×moravica* and 2:1 in hexaploid *F. ×bohemica*). In agreement with this assumption, we also noticed that *F. ×moravica* compared to *F. ×bohemica* could be characterised by a denser indumentum of the upper side of leaves (Fig. 10A) and the basal part of the leaf petioles (Fig. 10C) and by larger hairs on the veins on the lower sides of the leaves (Figs. 10B & 10E). *Fallopia ×moravica* could also be distinguished from *F. ×bohemica* by other morphological traits, e.g., more undulate (wavy) leaf edges (see also Hollingsworth *et al.* 1999) and more intense purple colouration of the veins on the lower sides of leaves and petioles (both traits are noticeable, especially in fully dazzled individuals), although the variability of these characters is considerable (Figs. 9A-D). A more thorough evaluation of the relevance of these traits will require statistical evaluation on a larger amount of study material.
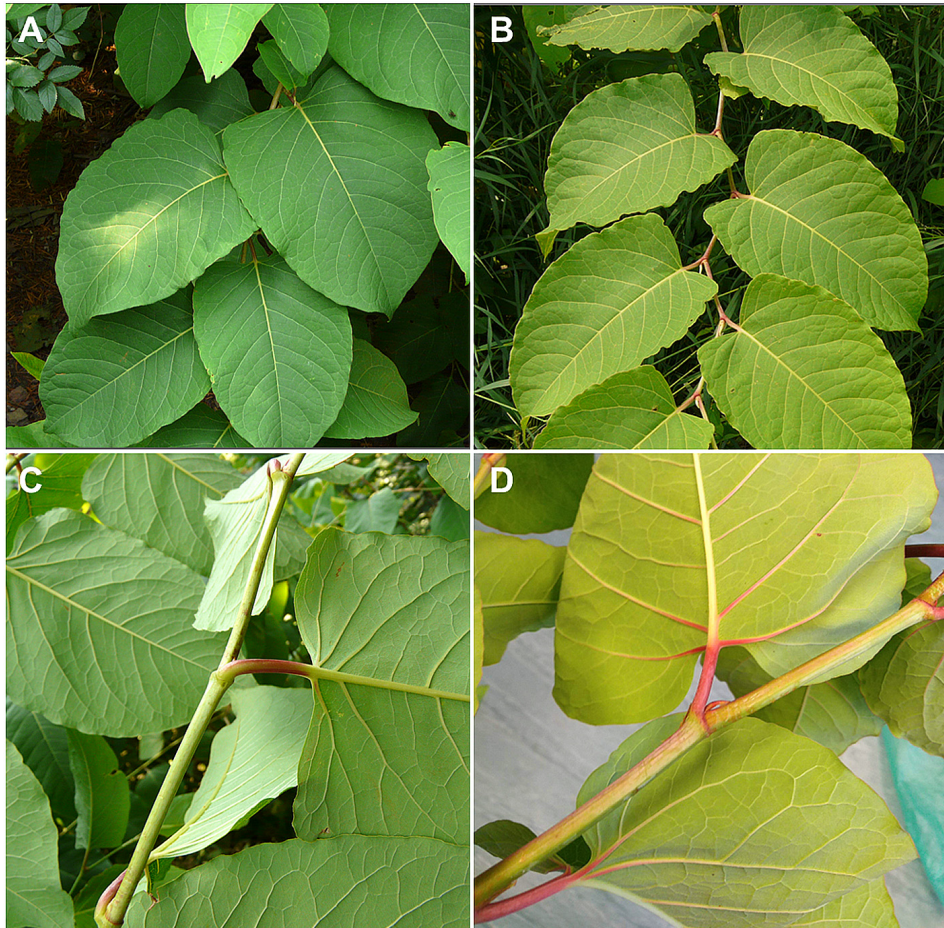
FIGURE 9. A., B. Variability in the intensity of the undulation (wavy) of leaf edges in *Fallopia ×moravica*. – **C., D.** Variability in the intensity of the purple colouration of the lower side of leaves and petioles in *Fallopia ×moravica*. Photos by Mereďa, P. Jr.

Variation in *Fallopia ×moravica*:—All stands from the Moravian localities in which we had the opportunity to observe flowers (58% of stands) were male fertile, i.e., all flowers have a small pistil and long stamens, well exserted from the perianth. Such flowers are functionally/effectively male or hermaphrodite and their detailed structure was already documented on electron micrographs in Bailey (1989: 63, the taxon is reported there as "tetraploid *Reynoutria*") and Desjardins (2015: 170, as "hermaphrodite *Reynoutria ×bohemica*"; in Desjardins *et al*. 2022: 6 as "Japanese knotweed s.l."). We did not observe flowers on Moravian stands that were either on private land (stands no. 1074-5, 1074-6) or were repeatedly mowed before flowering (stands no. 495-3, 496-2, 497-1, 1074-4, 1074-7, 1074-8, 1074-11, 1075-1, 1075-2, 1077, 1081-4, 1083-1; Fig. 11). As we observed at least one flowering stand at almost all sites, we assume that all the *F. ×moravica* stands in Račice and Olomouc are male fertile. Except for male fertile individuals, male sterile plants were also reported within *F. ×moravica* from other parts of the hybrid range, namely, from England (Bailey *et al*. 1996, as "tetraploid *F. ×bohemica*") and the South Island of New Zealand (Desjardins 2015 and Desjardins *et al*. 2022, as "tetraploid *Reynoutria ×bohemica*"); such plants could also be found in the Czech Republic in the future.

Bailey (1989: 228) and Bailey & Wisskirchen (2006) reported that artificial hybrids of tetraploid *Fallopia compacta* (reported as *F. japonica* var. *compacta*) and tetraploid *F. sachalinensis* are very diverse, and it seemed that the mother plant (whether it was *F. compacta* or *F. sachalinensis*) had strong effects on the phenology and morphology of progeny. Bailey (1989: 228) reports that if *F. sachalinensis* (reported as *Reynoutria sachalinensis*) was the female parent in the artificial hybridisation, then the hybrid plant was readily distinguished from reciprocal hybrids by their "smaller height, up to 1.5 m, and by their much earlier onset of flowering" (early to mid-August in England). In contrast, Pashley (2003: 104), in the case of very tall hybrid plants (growing up to 4 m), supposed that such tall plants could be the result of having *F. sachalinensis* as the maternal parent. It seems that, at least based on the height of the *F. ×moravica* plants, it is not possible to reliably estimate their maternal parent.

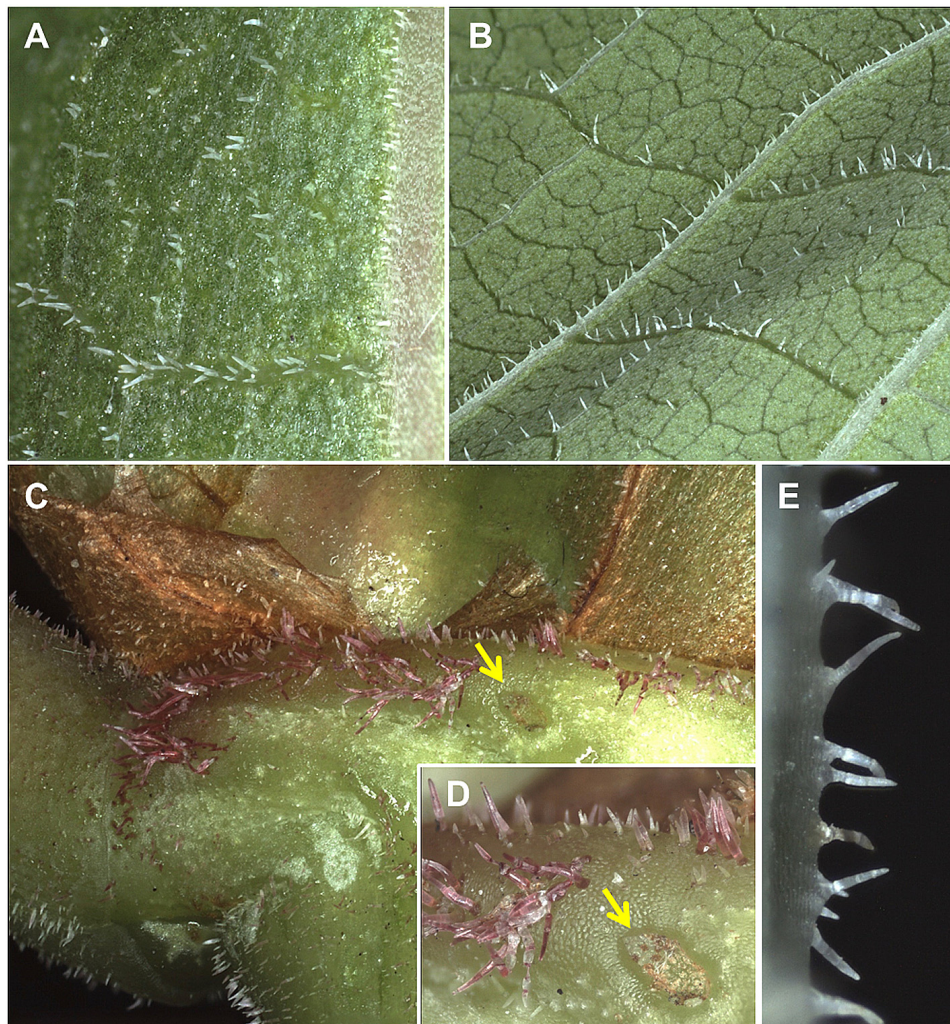**FIGURE 10.** Leaf indumentum in *Fallopia ×moravica*. – **A.** Upper side of a leaf. – **B.** Lower side of a leaf. – **C.** Hairs on the base of a leaf petiole from the middle part of the stem. – **D.** Detailed view of the base of a leaf petiole with an extrafloral nectary (yellow arrow). – **E.** Detailed view of the hairs on a leaf underside. Photos by Mereďa, P. Jr.

Although *Fallopia ×moravica* plants from Řečice and Olomouc represent at least two different genotypes (Mandák *et al.* 2005: 224) morphologically they are quite uniform. Interestingly, both Pashley (2003) and Desjardins (Desjardins 2015, Desjardins *et al.* 2022), when studying hybrids between *F. compacta* and *F. sachalinensis* in England and the South Island of New Zealand, respectively, also detected several different genotypes within the plants, even at one site. Unfortunately, the abovementioned studies do not report detailed data on the morphology of the studied plants (including the presence/absence of spots on the stem). At this time, *F. ×moravica* can be reliably distinguished from *F. ×bohemica* by the absence of purple spots on the stem (Fig. 8), different RGS (Table 2) and different number of chromosomes (2n = 44 vs. 2n = 66 or 88). However, as follows from the information provided by Bailey (1989), Pashley (2003), Bailey & Wisskirchen (2006), and Desjardins (2015), in the future, it can be expected that the morphological as well as cytological variability of *F. ×moravica* could be much greater than is currently presented. It cannot even be ruled out that some *F. ×moravica* genotypes may be hexa- or octoploid (depending on the fusion of reduced and nonreduced gametes of 4x *F. ×moravica* or parental taxa 4x *F. compacta* and 4x, 6x or 8x *F. sachalinensis*), or they may have spotted stem.

Distribution of the new hybrid:—To date, *Fallopia ×moravica* has been reported in several localities in England (Bailey & Conolly 1985, as "*Reynoutria* tetraploids", Bailey 1989, as "4x Hybrid *Reynoutria*", Bailey *et al.* 1996, 2007, as "tetraploid *F. ×bohemica*"), two localities in the Moravia region (Olomouc town and Račice village) in the Czech Republic (Mandák *et al.* 2003, Bailey & Wisskirchen 2006, Suda *et al.* 2010, Bailey 2013; reported as "tetraploid *Reynoutria ×bohemica*" or "tetraploid *F. ×bohemica*") and in several localities in New Zealand (the Tasman and West Coast Districts of the South Island; Desjardins 2015: 155–166, Desjardins *et al.* 2022, both reported as "tetraploid *Reynoutria ×bohemica*").
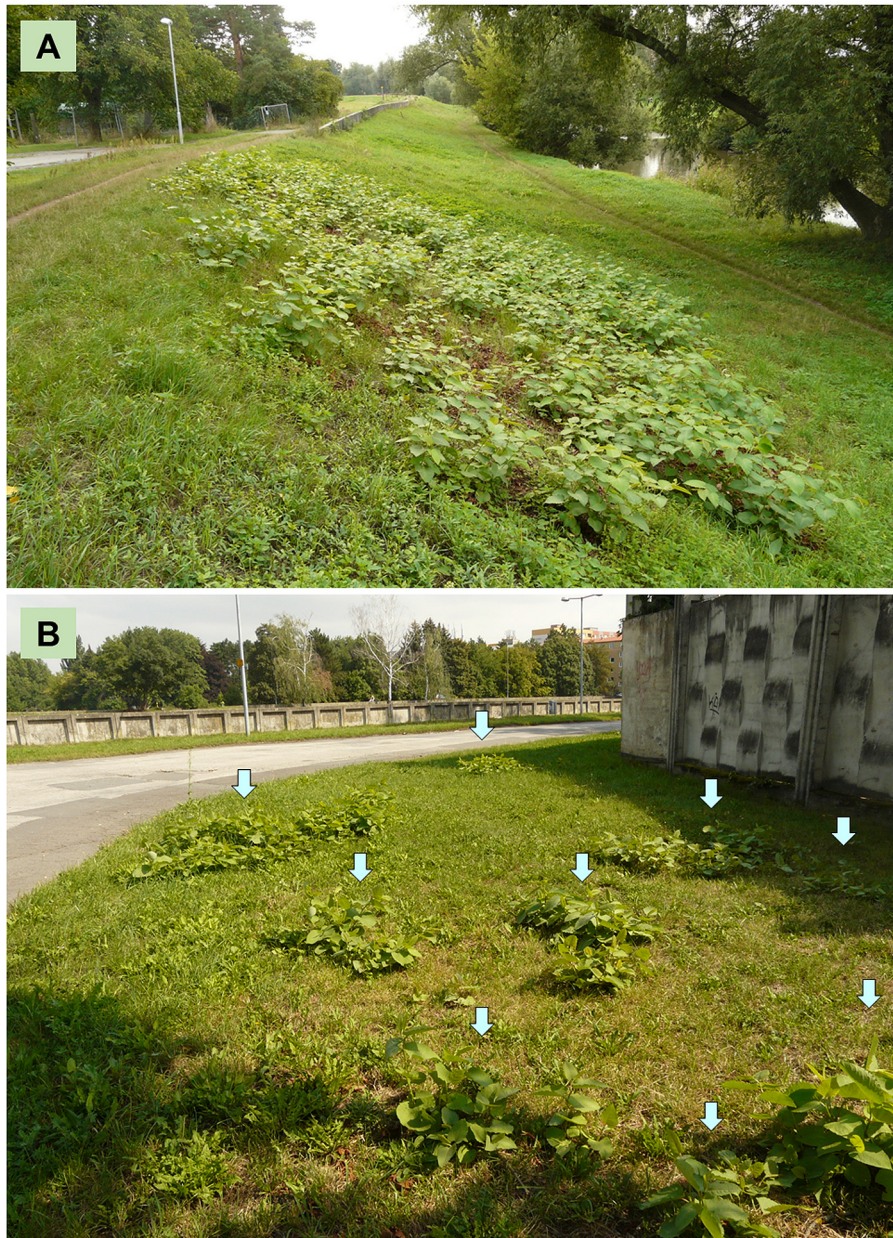
FIGURE 11. Mowed stands of *Fallopia ×moravica* in Olomouc town (Czech Republic). – **A.** Stand no. 1077 on the left embankment of the Morava River. – **B.** Stand no. 496-1 in grassland along the road. The stand numbers follow those in Table 1. Photos by Mereďa, P. Jr., 24 August 2022.

There are indications that *Fallopia ×moravica* could occur also in East Asia, as two *F. ×moravica* (reported as "tetraploid *F. ×bohemica*") genotypes found in New Zealand possessed chloroplast haplotype which was confirmed to Japan but has never been recorded in Europe or elsewhere in Australasia. These accessions could have been introduced to New Zealand (as the hybrid itself or one of its parental species) from East Asia by Chinese workers (Desjardins *et al.* 2022). In addition, Pashley (2003: 208, 219) reports chromosome number 2n = 44 for putative hybrid between "*F. sachalinensis* × 4x *F. japonica*" from Japan, although, the second parent was not identified in more detail (whether it was *F. compacta*, reported as "dwarf *F. japonica* var. *japonica*" or *F. japonica* s. str.).

In the Czech Republic and the United Kingdom, *Fallopia ×moravica* is rarer than hexaploid *F. ×bohemica* (in ratios of 1:43.5 and 1:3.6, respectively; cf. Mandák *et al.* 2003, Bailey & Wisskirchen 2006), and the opposite ratio was recorded in New Zealand by Desjardins (Desjardins 2015, Desjardins *et al.* 2022): four individuals of hexaploid *Reynoutria ×bohemica* and 11 individuals of tetraploid *Reynoutria ×bohemica* (i.e., *Fallopia ×bohemica* and *F. ×moravica* in our study).

We collected *Fallopia ×moravica* at both Moravian localities reported; in one of them, Olomouc, we found another 10 new sites of this hybrid (Table 1, Fig. 1). Because all studied populations of *F. ×moravica* are very vital,

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and most of them form multiple stands within one locality (see Fig. 1), the hybrid can very likely also occur in other sites in Moravia, especially in the Morava River alluvium. Due to the abovementioned occurrence of *F. ×moravica* in England and the South Island of New Zealand, we assume that the hybrid could also be discovered in other regions of Europe or the world.

Origin of *Fallopia ×moravica*:—The studied populations of *F. ×moravica* form monospecific stands without admixtures of other *F.* sect. *Reynoutria* representatives (only at sites no. 1193 and 1199, *F. japonica* var. *japonica* stands also occurred near *F. ×moravica* plants). Additionally, at no sites where *F. ×moravica* was found in Moravia, there was no evidence of its parental species (see also Mandák *et al.* 2003). *Fallopia compacta* was known only from five localities in the Czech Republic: two cultivated (one of them growing in Mariánske Lázně spa in the Bohemia region; cf. Hlaváček *et al.* 1996) and three in the wild (Mandák *et al.* 2003, Bailey *et al.* 2007, Suda *et al.* 2010). The three wild localities (all from Bohemia) located outside of cultivation (and the only ones with exact locations), namely, Příbram town, Litoměřice town and Rejštejn-Svojše borough (cf. Mandák *et al.* 2003, Suda *et al.* 2010), were visited in 2017 by P. Mereďa Jr.; however, the species was not found in any of these sites.

The tetraploid *Fallopia sachalinensis* has a scattered distribution in Moravia; however, there are no specific data on its occurrence in Račice or Olomouc or nearby (cf. Mandák *et al.* 2003). Therefore, it does not seem likely that the hybrid plants arose *in situ*. There is a high possibility that *F. ×moravica* was introduced to these sites from other area/areas of origin located either in other parts of the Czech Republic or in other European countries, including the United Kingdom, where the hybrid is relatively abundant (Bailey *et al.* 1996, Pashley 2003, both as "tetraploid *F. ×bohemica*"). A similar phenomenon was reported by Desjardins (Desjardins 2015, Desjardins *et al.* 2022), who, on the basis of molecular markers, identified that probably all tetraploid *Reynoutria ×bohemica* individuals (i.e., *F. ×moravica* in our study) collected in New Zealand were introduced there from either the United Kingdom or East Asia. However, it cannot be fully excluded that *F. compacta* and *F. sachalinensis* have occurred (or still occur) in the wild or are cultivated in gardens in Olomouc and/or Račice (or in their vicinity) in Moravia; thus, *F. ×moravica* could arise directly in at least one of these sites.

Invasive potential of the new hybrid:—The parental species of *Fallopia ×moravica* differ significantly in their invasive potential. *Fallopia compacta* is reported from its whole adventive range (Europe, North America, Australia, New Zealand) as a rare plant, with no or minimal invasiveness (Conolly 2001, Bailey 2003, Desjardins *et al.* 2022). In Europe, it has thus far been found in several countries, such as the United Kingdom, Ireland, Belgium, Netherlands, Germany, and the Czech Republic (Hlaváček *et al.* 1996, Bailey *et al.* 1996, 2007, Hollingsworth & Bailey 2000, Mandák *et al.* 2003, Bailey *et al.* 2007, Tiébré *et al.* 2007a, Balogh 2008, Galasso *et al.* 2009, Alberternst & Böhmer 2011, Duistermaat *et al.* 2012, Stace & Crawley 2015: 302). In contrast, *F. sachalinensis* is considered a dangerous invasive plant in many European countries (e.g., the United Kingdom, Belgium, Germany, Czech Republic, Poland, Slovakia), even though the number of its stands is significantly lower on the continent than those of *F. japonica* var. *japonica* or *F. ×bohemica* (Mandák *et al.* 2003, 2005, Bailey *et al.* 2007, Pashley *et al.* 2007, Šípošová 2016, Holm *et al.* 2018, Beringen *et al.* 2019). According to our observations, *F. ×moravica* has significant invasive potential, at least at the level of *F. sachalinensis*. In most studied Moravian localities, it creates several monospecific stands with diameters of 2 to 20 m, and for example, in the wider centre of Olomouc, it belongs to the most frequent representatives of *F.* sect. *Reynoutria* (Mereďa Jr., ined.). Similar invasive ability of *F. ×moravica* was also recorded from England, where the hybrid is thought to be fully fertile (Hollingsworth *et al.* 1999, Pashley 2003), and in some English towns, it is a dominant knotweed taxon, showing signs of being more invasive than either of its parental taxa (Pashley 2003: 91, 310). In this regard, Pashley (2003: 109) reproduces an illustrative photo of *F. ×moravica* (reported as "tetraploid *F. ×bohemica*") stand from Preston (U.K.), which is 4 m tall and covers an area of approximately 2,250 m^2.

Importance of *Fallopia ×moravica* in knotweed evolution:—Description of the new *Fallopia* taxon, *F. ×moravica*, in connection with an unclear situation in the systematics of *F. japonica* in East Asia, as well as other consequences resulting from the raising of *F. japonica* var. *compacta* to the species level (as *F. compacta*), show the need for deeper taxonomic research of *F.* sect. *Reynoutria* in both its native and adventive distribution areas. In relation to *F. ×moravica*, significant findings are that the hybrid appears to be capable of backcrossing with their parents, which both have the same chromosome number (2n = 44) (Bailey 2003, Bailey *et al.* 2009). The limiting factor of *F. ×moravica* occurrence is presumably only the scarcity of the *F. compacta* parent (Pashley 2003: 106). *Fallopia ×moravica* is also able to cross with the distantly related knotweed species *F. baldschuanica* (2n = 20), a member of *F.* sect. *Sarmentosae*, which is different in not only ploidy level but also basic chromosome number (Bailey 1988, 1989, 2003, 2013, Bailey & Stace 1992, Bailey *et al.* 2009, Pashley *et al.* 2007, Desjardins 2015). Thus, hybridisation of *F. ×moravica* with closely related *Fallopia* species from the same section of *F.* sect. *Reynoutria*, namely, *F. japonica* var. *japonica* (2n = 88) and *F. ×bohemica* (2n = 66 or 88), is also highly probable. Regarding the relatively abundant

occurrence of *F. ×moravica* in some regions of the world (e.g., England, the South Island of New Zealand, Olomouc town, see above) and its crossing ability, higher attention should be given to this hybrid, not only from the weed control perspective but also from evolutionary biology (incl. invasion dynamics) of the whole *Fallopia* genus (e.g., Hollingsworth *et al*. 1999, Pashley 2003).

Acknowledgments

References

Adanson, M. (1763) *Families des plantes*, vol. 2. Vincent, Paris, 640 pp.
https://doi.org/10.5962/bhl.title.271

Alberternst, B. & Böhmer, H.J. (2011) NOBANIS – Invasive alien species fact sheet – *Fallopia japonica. In:* European Network on Invasive Alien Species (NOBANIS) *Online database of the European network on invasive alien species*. Available from: https://www.nobanis.org/globalassets/speciesinfo/r/reynoutria-japonica/reynoutria_japonica4.pdf (accessed 11 April 2017).

Bailey, J.P. (1988) Putative *Reynoutria japonica* Houtt. × *Fallopia baldschuanica* (Regel) Holub hybrids discovered in Britain. *Watsonia* 7: 163–164.

Bailey, J.P. (1989) *Cytology and breeding behaviour of giant alien Polygonum species in Britain*. PhD thesis, University of Leicester, Leicester, 380 pp.

Bailey, J.P. (2001) *Fallopia ×conollyana* the railway-yard knotweed. *Watsonia* 23: 539–541.

Bailey, J.P. (2003) Japanese knotweed s.l. at home and abroad. *In*: Child, L.E., Brock, J.H., Brundu, G., Prach, K., Pyšek, P., Wade, P.M. & Williamson, M, (eds.) *Plant invasions: ecological threats and management solutions*. Backhuys Publishers, Leiden, pp. 183–196.

Bailey, J.P. (2013) The Japanese knotweed invasion viewed as a vast unintentional hybridisation experiment. *Heredity* 110: 105–110.
https://doi.org/10.1038/hdy.2012.98

Bailey, J.P., Bímová, K. & Mandák, B. (2007) The potential role of polyploidy and hybridisation in the further evolution of the highly invasive *Fallopia* taxa in Europe. *Ecological Research* 22: 920–928.
https://doi.org/10.1007/s11284-007-0419-3

Bailey, J.P., Bímová, K. & Mandák, B. (2009) Asexual spread versus sexual reproduction and evolution in Japanese knotweed s.l. sets the stage for the "Battle of the clones". *Biological Invasions* 11: 1189–1203.
https://doi.org/ 10.1007/s10530-008-9381-4

Bailey, J.P., Child, L.E. & Conolly, A.P. (1996) A survey of the distribution of *Fallopia × bohemica* (Chrtek & Chrtková) J. Bailey (Polygonaceae) in the British Isles. *Watsonia* 21: 187–198.

Bailey, J.P. & Stace, C.A. (1992) Chromosome number, morphology, pairing, and DNA values of species and hybrids in the genus *Fallopia* (Polygonaceae). *Plant Systematics and Evolution* 180: 29–52.
https://doi.org/10.1007/BF00940396

Bailey, J.P. & Wisskirchen, R. (2006) The distribution and origins of *Fallopia ×bohemica* (Polygonaceae) in Europe. *Nordic Journal of Botany* 24: 173–199.
https://doi.org/10.1111/j.1756-1051.2004.tb00832.x

Balant, M. (2015) *Potencialno invazivni vrsti Fallopia baldschuanica in Fallopia multiflora v Sloveniji*. Msc thesis, Biotehniška fakulteta Univerza v Ljubljani, Ljubljana, 95 pp.

Balogh, L. (2008) Japanese, giant and Bohemian knotweed (*Fallopia japonica* (Houtt.) Ronse Decr., *F. sachalinensis* (Frdr. Schmidt) Ronse Decr. and *F. ×bohemica* (Chrtek et Chrtková) J. P. Bailey). *In*: Botta-Dukát, Z. & Balogh, L. (eds.) *The most important invasive plants in Hungary*. Institute of Ecology and Botany, Hungarian Academy of Sciences, Vácrátót, pp. 13–33.

Beerling, D.J., Bailey, J.P. & Conolly, A.P. (1994) *Fallopia japonica* (Houtt.) Ronse Decraene. *Journal of Ecology* 82: 959–979.
https://doi.org/10.2307/2261459

Beringen, R., Leuven, R.S.E.W., Odé, B., Verhofstad, M. & van Valkenburg, J.L.C.H. (2019) *Risk assessment of four Asian knotweeds in Europe. FLORON report 2018.049.e1*. FLORON, Nijmegen, pp. 1–113.

Bímová, K., Mandák, B. & Pyšek, P. (2001) Experimental control of *Reynoutria* congeners: a comparative study of a hybrid and its parents. *In:* Brundu, G., Brock, J., Camarda, I., Child, L. & Wade, M. (Eds.) *Plant Invasions: Species Ecology and Ecosystem*

Management. Backhuys, Leiden, pp. 283–290.

Bímová, K., Mandák, B. & Pyšek, P. (2003) Experimental study of vegetative regeneration in four invasive *Reynoutria* taxa (Polygonaceae). *Plant Ecology* 166: 1–11.
https://doi.org/10.1023/A:1023299101998

Bzdega, K., Janiak, A., Książczyk, T., Lewandowska, A., Gancarek, M., Sliwinska, E. & Tokarska-Guzik, B. (2016) A survey of genetic variation and genome evolution within the invasive *Fallopia* complex. *PLoS ONE* 11 (8): e0161854.
https://doi.org/10.1371/journal.pone.0161854

Chrtek, J. & Chrtková, M. (1983) *Reynoutria ×bohemica*, nový kříženec z čeledi rdesnovitých. *Časopis Národního Muzea v Praze, Řada Přírodovědná* 152 (2): 120.

Conolly, A.P. (2001) Japanese knotweeds in Australia. *BSBI News* 87: 74–75.

Cunningham, A. (1838) Florae insularum Novae Zelandiae precursor; or a specimen of the botany of the Islands of New Zealand. *Annals of Natural History* 1: 455–462.
https://doi.org/10.1080/00222933809496630

Desjardins, S.D. (2015) *Evolutionary studies in subtribe Reynoutriineae (Polygonaceae)*. PhD thesis, University of Leicester, Leicester.

Desjardins, S.T., Pashley, C.H. & Bailey, J.P. (2022) A taxonomic, cytological and genetic survey of Japanese knotweeds s.l. in New Zealand indicates multiple secondary introductions from Europe and a direct introduction from Japan. *New Zealand Journal of Botany*: 1–18.
https://doi.org/10.1080/0028825X.2022.2090848

Duistermaat, H., Soes, D.M., van Valkenburg, J., van Heuven, B.J., Zonneveld, B. & Kessler, P.J.A. (2012) *Actuele verspreiding en risico's van mannelijk fertiele Fallopia japonica (Polygonaceae) planten.* NCB Naturalis, Leiden.

Galasso, G., Banfi, E., De Mattia, F., Grassi, F., Sgorbati, S. & Labra, M. (2009) Molecular phylogeny of *Polygonum* L. s.l. (Polygonoideae, Polygonaceae), focusing on European taxa: preliminary results and systematic considerations based on *rbc*L plastidial sequence data. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 150: 113–148.

Gillies, S., Clements, D.R. & Grenz, J. (2016) Knotweed (*Fallopia* spp.) invasion of North America utilizes hybridization, epigenetics, seed dispersal (unexpectedly), and an arsenal of physiological weapons. *Invasive Plant Science and Management* 9: 71–80.
https://doi.org/10.1614/IPSM-D-15-00039.1

Greilhuber, J., Doležel, J., Lysák, M.A. & Bennett, M.D. (2005) The origin, evolution and proposed stabilization of the terms 'Genome size' and 'C-value' to describe nuclear DNA contents. *Annals of Botany (Oxford)* 95: 255–260.
https://doi.org/10.1093/aob/mci019

Groom, Q. (2011) *Reynoutria* compacta. *In*: Verloove, F. (Ed.) *Manual of the Alien Plants of Belgium*. Botanic Garden Meise, Meise. Available from: https://alienplantsbelgium.myspecies.info/content/reynoutria-compacta (accessed 30 August 2021).

Gușuleac, M. (1952) Addenda diagnoses plantarum novarum in tomo I Florae R.P.R. commemoratarum. *In*: Săvulescu, T. (Ed.) *Flora Republicii populare Române I*. Academia Reipublicii populare Române, București, pp. 633–645.

Haraldson, K. (1978) Anatomy and taxonomy in Polygonaceae subfam. Polygonoideae Meisn. emend. Jaretzky. *Symbolae Botanicae Upsalienses; Arbeten Fran Botaniska Institutionen i Uppsala. Uppsala* 22 (2): 1–95.

Hlaváček, R., Mandák, B. & Pyšek, P. (1996) Několik poznámek k nálezu *Reynoutria japonica* var. *compacta* v České republice. *Zprávy České Botanické Společnosti* 31: 167–171.

Hollingsworth, M.L. & Bailey, J.P. (2000) Hybridisation and clonal diversity in some introduced *Fallopia* species (Polygonaceae). *Watsonia* 23: 111–121.

Holm, A.-L., Elameen, A., Oliver, B.W., Brandsæter, L.O., Fløistad, I.S. & Brurberg, M.B. (2018) Low genetic variation of invasive *Fallopia* spp. in their northernmost European distribution range. *Ecology and Evolution* 8: 755–764.
https://doi.org/10.1002/ece3.3703

Holub, J. (1971) *Fallopia* Adans. 1763 instead of *Bilderdykia* Dum. 1827. *Folia Geobotanica et Phytotaxonomica* 6: 171–177.
https://doi.org/10.1007/BF02851760

Honda, M. (1932) Nuntia ad floram Japoniae XIX. *The Botanical Magazine, Tokyo* 46: 675–678.
https://doi.org/10.15281/jplantres1887.46.675

Hooker, J.D. (1880) Plants of the Royal Gardens of Kew. *Curtis's Botanical Magazine* 106: t. 6476.

Houttuyn, M. (1777) *Natuurlijke Historie, part 2, fasc. 8.* De Erven van F. Houttuyn, Amsterdam, 784 pp.

Keil, P. & Fuchs, R. (2019) Ein Vorkommen von *Fallopia ×conollyana* (Polygonaceae) in Essen (Nordrhein-Westfalen). *Floristische Rundbriefe* 53: 2–11.

Kim, J.Y. & Park, C.W. (2000) Morphological and chromosomal variation in *Fallopia* section *Reynoutria* (Polygonaceae) in Korea. *Brittonia* 52: 34–48.
https://doi.org/10.2307/2666492

Lavoie, C. (2017) The impact of invasive knotweed species (*Reynoutria* spp.) on the environment: review and research perspectives.

Biological Invasions 19: 2319–2337.
https://doi.org/10.1007/s10530-017-1444-y

Linnaeus, C. (1753) *Species plantarum,* vols. 1–2. Impensis Laurentii Salvi, Holmiae [Stockholm], 1200 pp.

Linnaeus, C. (1762) *Species plantarum,* ed. 2, vol. 1. Impensis Laurentii Salvii, Holmiae, [Stockholm], 784 pp.

Loos, G.H. (2010) Taxonomische Neukombinationen zur Flora Mittel- und Osteuropas, insbesondere Nordrhein-Westfalens. *Jahrbuch des Bochumer Botanischen Vereins* 1: 114–133.

Löve, Á. (1970) Emendations in the Icelandic Flora. *Taxon* 19: 298**–**302.
https://doi.org/10.2307/1217990

Makino, T. (1928) A contribution to the knowledge of the flora of Japan. *Journal of Japanese Botany* 5: 1–48.

Mandák, B. & Pyšek, P. (2019) *Reynoutria* Houtt. – křídlatka. *In*: Kaplan, Z., Danihelka, J., Chrtek, J.Jr., Kirschner, J., Kubát, K., Štech, M. & Štěpánek, J. (Eds.) *Klíč ke květeně České republiky, Ed. 2*. Academia, Praha, pp. 688–690.

Mandák, B., Bímová, K., Pyšek, P., Štěpánek, J. & Plačková, I. (2005) Isoenzyme diversity in *Reynoutria* (Polygonaceae) taxa: escape from sterility by hybridization. *Plant Systematics and Evolution* 253: 219–230.
https://doi.org/10.1007/s00606-005-0316-6

Mandák, B., Pyšek, P., Lysák, M., Suda, J., Krahulcová, A. & Bímová, K. (2003) Variation in DNA-ploidy levels of *Reynoutria* taxa in the Czech Republic. *Annals of Botany* 92: 265–272.
https://doi.org/10.1093/aob/mcg141

Maximowicz, C.J. (1859) Primitiae florae Amurensis, versuch einer flora des Amur-Landes. *Mémoires présentés a l'Académie Impériale des sciences de St.-Pétersbourg par divers savants et lus dans ses assemblées* 9: 1–504.

Meisner, C.F. (1841a) *Plantarum vascularium genera, part 1*. Libraria Weidmannia, Lipsiae [Leipzig], 442 pp.
https://doi.org/10.5962/bhl.title.44043

Meisner, C.F. (1841b) *Plantarum vascularium genera, part 2*. Libraria Weidmannia, Lipsiae [Leipzig], 402 pp.
https://doi.org/10.5962/bhl.title.44043

Mereďa, P.Jr., Koláriková, Z. & Hodálová, I. (2019a) Cytological and morphological variation of *Fallopia* sect. *Reynoutria* taxa (*Polygonaceae*) in the Krivánska Malá Fatra Mountains (Slovakia). *Biologia (Bratislava)* 74: 215–236.
https://doi.org/10.2478/s11756-018-00168-w

Mereďa, P.Jr., Majerová, M., Somlyay, L., Pekárik, L. & Hodálová, I. (2019b) Genome size variation in the Western Carpathian *Sesleria* (Poaceae) species. *Plant Systematics and Evolution* 305: 845–864.
https://doi.org/10.1007/s00606-019-01622-1

Moravcová, L., Pyšek, P., Jarošik, V. & Zákravský, P. (2011) Potential phssssesytotoxic and shading effects of invasive *Fallopia* (Polygonaceae) taxa on the germination of native dominant species. *NeoBiota* 9: 31–47.
https://doi.org/10.3897/neobiota.9.1266

Murín, A. (1960) Substitution of cellophane for glass covers to facilitate preparation of permanent squashes and smears. *Stain Technology* 35: 351–353.

Murray, J.A. (1784) *Caroli a Linneì equitis Systema vegetabilium etc., Ed. 14*. Typis et impensis Jo. Christ. Dieterich, Gottingae, 987 pp.
https://doi.org/10.5962/bhl.title.549

Park, Ch.-W., Bhandari, G.S., Won, H., Park, J.H. & Park, D.S. (2018) Polyploidy and introgression in invasive giant knotweed (*Fallopia sachalinensis*) during the colonization of remote volcanic islands. *Scientific Reports* 8: 16021.
https://doi.org/10.1038/s41598-018-34025-2

Pashley, C.H. (2003) The use of molecular markers in the study of the origin and evolution of Japanese knotweed sensu lato. PhD thesis, University of Leicester, Leicester, 344 pp.

Pashley, C.H., Bailey, J.P. & Ferris, C. (2007) Clonal diversity in British populations of the alien invasive giant knotweed, *Fallopia sachalinensis* (F. Schmidt) Ronse Decraene, in the context of European and Japanese plants. *Watsonia* 26: 359–371.

Pyšek, P., Brock, J.H., Bímová, K., Mandák, B., Jarošík, V., Koukolíková, I., Pergl, J. & Štěpánek, J. (2003) Vegetative regeneration in ivasive *Reynoutria* (*Polygonaceae*) taxa: the determination of invasibility at the genotype level. *American Journal of Botany* 90: 1487–1495.
https://doi.org/10.3732/ajb.90.10.1487

Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, D.F. & West, C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6: 93–107.
https://doi.org/10.1046/j.1472-4642.2000.00083.x

Regel, E. (1884) Descriptiones plantarum novarum et minus cognitarum, fasc. IX. B. Descriptiones et emendationes plantarum bucharicarum turkestanicarumque. *Trudy Imperatorskago S.-Peterburgskago Botaniceskago Sada [Acta Horti Petropolitani]* 8: 645–702 + 21 figs.

Ronse Decraene, L.-P. & Akeroyd, J.R. (1988) Generic limits in *Polygonum* and related genera (Polygonaceae) on the basis of floral

characters. *Botanical Journal of the Linnean Society* 98: 321–371.
https://doi.org/10.1111/j.1095-8339.1988.tb01706.x

Saad, L., Tiébré, M.-S., Hardy, O.J., Mahy, G. & Vanderhoeven, S. (2011) Patterns of hybridization and hybrid survival in the invasive alien *Fallopia* complex (Polygonaceae). *Plant Ecology Evolution* 114: 12–18.
https://doi.org/10.5091/plecevo.2011.444

Schönswetter, P., Suda, J., Popp, M., Weiss-Schneeweiss, H. & Brochmann, C. (2007) Circumpolar phylogeography of *Juncus biglumis* (Juncaceae) inferred from AFLP fingerprints, cpDNA sequences, nuclear DNA content and chromosome numbers. *Molecular Phylogenetics and Evolution* 42: 92–103.
https://doi.org/10.1016/j.ympev.2006.06.016

Schuster, T.M., Wilson, K.L. & Kron, K.A. (2011) Phylogenetic relationships of *Muehlenbeckia*, *Fallopia*, and *Reynoutria* (Polygonaceae) investigated with chloroplast and nuclear sequence data. *International Journal of Plant Sciences* 172: 1053–1066.
https://doi.org/10.1086/661293

Sell, P. & Murrell, G. (2018) *Flora of Great Britain and Ireland. Volume 1. Lycopodiaceae – Salicaceae*. Cambridge University Press, Cambridge, 787 pp.

Shimoda, M. & Yamasaki, N. (2016) *Fallopia japonica* (Japanese Knotweed) in Japan: why is it not a pest for Japanese people? *In*: Box, E.O. (Ed.) *Vegetation structure and function at multiple spatial, temporal and conceptual scales*. Geobotany Studies. Springer, Cham, pp. 447–473.
https://doi.org/10.1007/978-3-319-21452-8_20

Stace, C.A. & Crawley, M.J. (2015) *Alien Plants*. William Collins, London, 626 pp.

Stalažs, A. (2022) The first findings of invasive *Reynoutria ×bohemica* Chrtek & Chrtková (Polygonaceae) in Latvia. *Botany Letters* 169: 119–126.
https://doi.org/10.1080/23818107.2021.1981438

Suda, J., Trávníček, P., Mandák, B. & Berchová-Bímová, K. (2010) Genome size as a marker for identifying the invasive alien taxa in *Fallopia* section *Reynoutria*. *Preslia* 82: 97–106.

Šípošová, H. (2016) *Reynoutria* Houtt. Krídlatka (pohánkovec). *In*: Goliašová, K. & Michalková, E. (Eds.) *Flóra Slovenska VI/4*. Veda, Bratislava, pp. 485–497.

Tiébré, M.-S., Bizoux, J.P., Hardy, O.J., Bailey, J.P. & Mahy, G. (2007a) Hybridization and morphogenetic variation in the invasive alien *Fallopia* (Polygonaceae) complex in Belgium. *American Journal of Botany* 94: 1900–1910.
https://doi.org/10.3732/ajb.94.11.1900

Tiébré, M.S., Vanderhoeven, S., Saad, L. & Mahy, G. (2007b) Hybridization and sexual reproduction in the invasive alien *Fallopia* (Polygonaceae) complex in Belgium. *Annals of Botany (Oxford)* 99: 193–203.
https://doi.org/10.1093/aob/mcl242

Tison, J.M., Abdulhak, S., Bock, B., Boudrie, M., Fridlender, A., Roccia, A., Van Es, J. & Véla, E. (2021) Combinaisons nouvelles requises dans la seconde édition de Flora Gallica. *Evaxiana* 8: 220–225.

Yonekura, K. & Ohashi, H. (1997) New combinations of East Asian species of *Polygonum* s.l. *Journal of Japanese Botany* 72: 154–161.