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A survey of the distribution of *Fallopia* × *bohemica* (Chrtek & Chrtková) J. Bailey (Polygonaceae) in the British Isles

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ABSTRACT

A recording form including details of how to identify *Fallopia* × *bohemica* (Chrtek & Chrtková) J. Bailey (*F. japonica* × *F. sachalinensis*) was circulated to botanists. The results from this survey, and previously collected data from the University of Leicester, are presented here, with ploidy level and sex expression of the hybrids where known. The origins, distribution pattern, sex expression and possible consequences of the presence of the hybrids in the British Isles are discussed.

KEYWORDS: Japanese knotweeds, *Polygonum cuspidatum*, *Reynoutria japonica*, hybridisation.

INTRODUCTION

Fallopia japonica (Houtt.) Ronse Decraene var. *japonica* (*Reynoutria japonica* Houtt. var. *japonica*) (Polygonaceae) was introduced to Britain in the first half of the nineteenth century from Japan, most probably through the nursery garden of Philipp Franz von Siebold at Leiden. It appears that only the male-sterile clone was introduced, and consequently all seed produced by it is inevitably hybrid (Bailey 1994). *F. sachalinensis* (F. Schmidt ex Maxim.) Ronse Decraene, a native of southern Sakhalin and northern Japan, is assumed to have been introduced in 1869 (Conolly 1977). The hybrid between *F. japonica* and *F. sachalinensis* is called *Fallopia* × *bohemica* Chrtek & Chrtková) J. Bailey, and was first described in 1983 (*Reynoutria* × *bohemica* Chrtek & Chrtková) from the town of Náchod in northeastern Bohemia, Czech Republic. The identification was made solely on the basis of morphological characters. Bailey & Conolly (1985) suggested that six hexaploid ($2n = 66$) and three tetraploid ($2n = 44$) plants they had examined were probably hybrids between *F. japonica* and *F. sachalinensis*. Production of, and comparison with, a range of artificial hybrids produced at the University of Leicester strongly supported this identification (Bailey 1989). The interpretation of the two different ploidy levels in *F.* × *bohemica* is that the hexaploid hybrid is a cross between *F. japonica* var. *japonica* ($2n = 88$) and *F. sachalinensis* ($2n = 44$), whilst the tetraploid is a cross between *F. japonica* var. *compacta* (Hook. f.) J. Bailey ($2n = 44$) and *F. sachalinensis* (Bailey 1989).

By 1989 the number of wild hybrids known in the British Isles and studied cytologically had increased to 16 hexaploids and 4 tetraploids. Further, a significant number of the hexaploids were male-fertile and indeed, even today, the best and most convenient means of initial hybrid recognition is to spot male-fertile plants. During succeeding years additional records were accumulated at the University of Leicester and from the B.S.B.I. county recorders; of particular note are the considerable number of records made by the Surrey Flora Committee. Unfortunately, despite access to artificial hybrids, we are still unable to distinguish unequivocally the 4x and 6x hybrids using any character other than chromosome number. It may be possible to use trichome characters, since the different proportions of *F. japonica* to *F. sachalinensis* genomes (2:1 in the hexaploid and 1:1 in the tetraploid) do appear to have an effect on the relative lengths and frequencies of the different lower epidermal trichomes. This possibility has not yet been fully explored. Another potential method is the use of various DNA "fingerprinting" techniques; work at the University of Leicester is currently evaluating this possibility. Here we are combining the results of our earlier cytological research (Bailey & Stace 1991) with records based solely on morphological identification. We have personally examined herbarium material for all the locations cited, except those reported by Miss V. Gordon and Dr Alan Leslie which we have taken on trust. This does mean that a number of locations are without chromosome data. Herbarium specimens for almost all the accessions in Table 2 are at **LTR**.

Although the hybrid can be readily distinguished from its parents, the key differences are not widely available. This, and the reluctance of some botanists to concern themselves with aliens, has led us to suspect that *F.* × *bohemica* may be an under-recorded element of the British and Irish flora. Even in the distribution maps produced by Conolly (1977), some *F. japonica* and *F. sachalinensis* records may have been *F.* × *bohemica*. Although no research has been done on the vegetative vigour of *F.* × *bohemica*, there is no reason to think it any less vigorous than *F. japonica* var. *japonica*, and its larger leaf size and stature may indicate that the hybrid has a higher productivity. *F. japonica* var. *japonica* itself has been examined as a potential biomass crop (Callaghan *et al.* 1984).

SURVEY METHODS

In order to obtain a better idea of the distribution and abundance of *F.* × *bohemica* in the British Isles an information sheet detailing the key points of recognition plus a standard recording form were produced and circulated to B.S.B.I. members in Autumn 1993. Additional, modified sheets were produced and circulated to members of the Arboricultural Advisory and Information Service (A.A.I.S.) and the Henry Doubleday Research Association (H.D.R.A.). This resulted in a total mailing of 4,700. The salient features of the information sheet are reproduced in Fig. 1 and Table 1.

In addition to the number of sites, we were also interested in the area occupied by the plant at each site, in order to give a very rough idea of its invasiveness. Requests for this information were included on the questionnaire, and additionally three well-known sites, two in Cirencester (E. Gloucs., v.c. 33) and one in Amroth (Pembs., v.c. 45), were visited and detailed measurements made of the extent of the hybrid plants.

This project featured at B.S.B.I. exhibition meetings in 1992 (Leicester & Loughborough Universities 1993), 1993 and 1994. The 1993 and 1994 exhibits were recorded by title only: *Japanese knotweed hybrid survey; results of the Leicester and Loughborough Universities joint research*, and *Unravelling the British distribution of Fallopia* × *bohemica*, respectively. This paper is a full account of the hybrid survey and covers material exhibited at all three meetings.

RESL

Over 300 replies were received, but not all respondents had correctly identified the hybrid. Some of the responses concerned previously compiled records not known to us but published in county Floras. The map (Fig. 2) shows the results of the survey, split into pre- and post-1993 records; those records identified as a direct result of our survey are shown as closed circles.

Table 2 gives details of all 126 localities that are separable by a six-figure grid reference. Most of these sites are on roadside verges, the remainder are along watercourses and in the grounds of large estates. There is no discernible difference between the habitats of *F.* × *bohemica* and its two parents. These records translate into 81 10-km records on the B.R.C. distribution map (Fig. 2), which shows fewer records than the table as many squares contain more than one site. This taxon was clearly an under-recorded element of the British and Irish flora, since 34 new sites have been

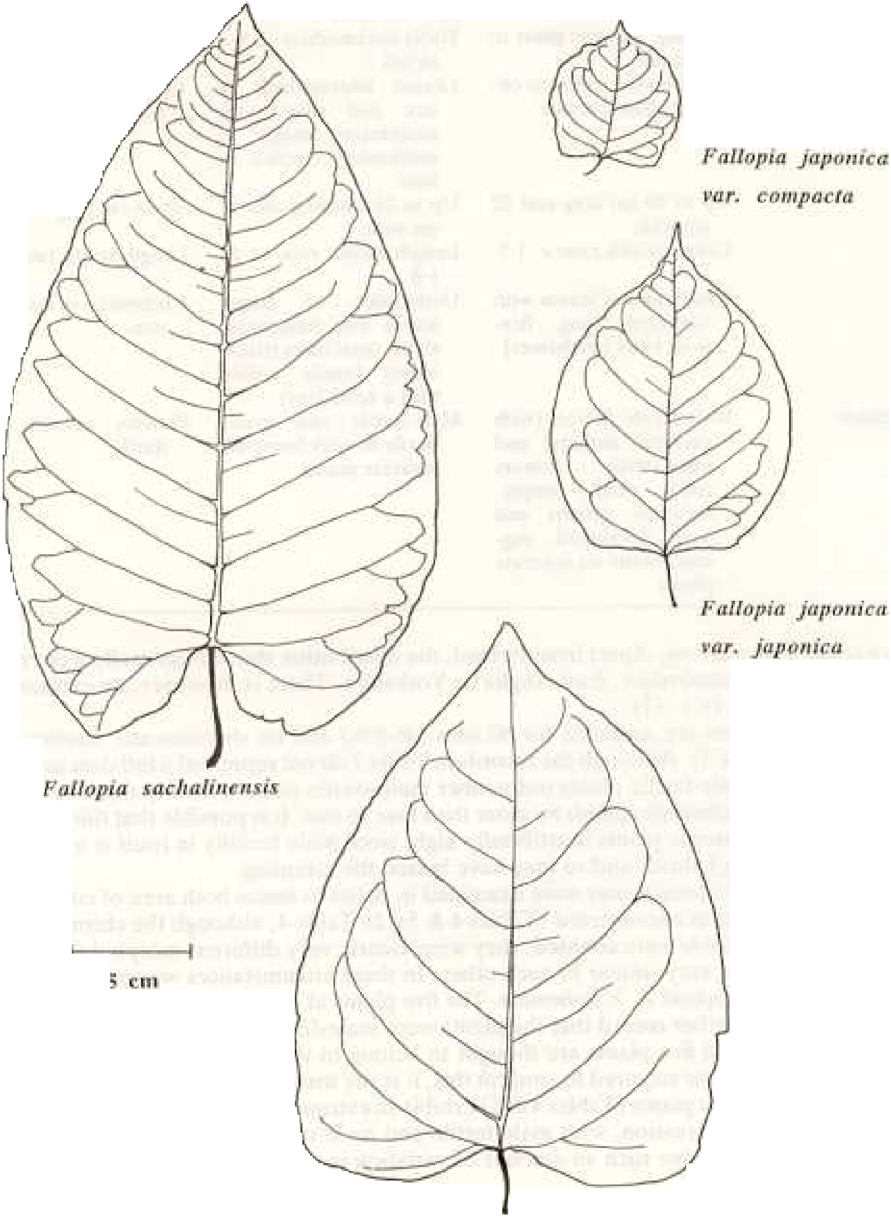

FIGURE 1. Leaves of *Fallopia japonica*, *F. sachalinensis* and *F.* × *bohemica* (after the illustration in the Japanese Knotweed Hybrid Survey leaflet).

TABLE DISTINGUISHING CHARACTERS OF *FALLOPIA* × *BOHEMICA* (TAKEN FROM THE TABLE IN THE HYBRID SURVEY LEAFLET, SEE TEXT FOR DETAILS)

Character	*F. sachalinensis*	*F.* × *bohemica*	*F. japonica* var. *japonica*
Chromosome number	2n = 44	2n = 66 or 44	2n = 88
Height	Striking, gigantic plant to 4 m tall	Habit intermediate, 2·5–4 m tall	Large plant, 2–3 m tall
Leaf characteristics	Basal leaves ovate to oblong, base cordate	Leaves intermediate in size and shape, tip acuminate, weakly to moderately cordate at base	Leaves ovate, acuminate, base truncate
	Up to 40 cm long and 22 cm wide	Up to 23 cm long and 19 cm wide	10–15 cm long
	Length:width ratio c. 1·5	Length:width ratio 1·1–1·8	Length:width ratio 1–1·5
	Undersides of leaves with scattered, long, flexuous hairs (trichomes)	Undersides of larger leaves with numerous, short, stout hairs (trichomes) (easily visible with a hand lens)	Undersides of leaves glabrous
Sex expression	Male-fertile flowers (with exserted anthers) and male-sterile flowers (with small, empty, included anthers and well developed stigmas) borne on separate plants	Male-fertile and male-sterile flowers borne on separate plants	Flowers usually male-sterile

added as a result of the survey. Apart from Ireland, the distribution shows a generally western bias, with no records from Lincolnshire, East Anglia or Yorkshire. There is, however, an extraordinary concentration in Surrey (v.c. 17).

Data on sex-expression are available for 60 sites (46·8%) and on chromosome number for 35 locations (27·7%) (Table 3). Although the records in Table 3 do not represent a full data set, certain trends are apparent. Male-fertile plants outnumber male-sterile ones by nearly three to one, and hexaploid clones outnumber tetraploids by more than four to one. It is possible that this proportion of male-fertile to male-sterile plants is artificially high, since male fertility in itself is a convenient character for identifying hybrids and so may have biased the sampling.

Three selected *F.* × *bohemica* sites were examined in detail to assess both area of cover and the amount of genetic variation encountered (Tables 4 & 5). In Table 4, although the chromosomes of only three of the hexaploids were counted, they were clearly very different morphologically from the single tetraploid, yet very similar to each other. In these circumstances we consider it safe to assign all of them to hexaploid *F.* × *bohemica*. The five plants at Amroth were not in flower at the time of the visit, so an earlier record that the plants were male-fertile and hexaploid was used. On morphological grounds all five plants are thought to belong to the same clone. Though evidence from DNA studies would be required to confirm this, it is the usual pattern at *F.* × *bohemica* sites. In contrast, the Cirencester plants (Tables 4 & 5) exhibit an extraordinary range of variation, both in ploidy level and in sex-expression, with male-fertile and male-sterile hexaploids and male-sterile tetraploids. To our knowledge such an amount of variation in a relatively small area is unique to Cirencester.

DISCUSSION

This survey establishes that *F.* × *bohemica* represents a significant component of the Japanese knotweed population in Britain, in terms of both numbers of records and area covered. At

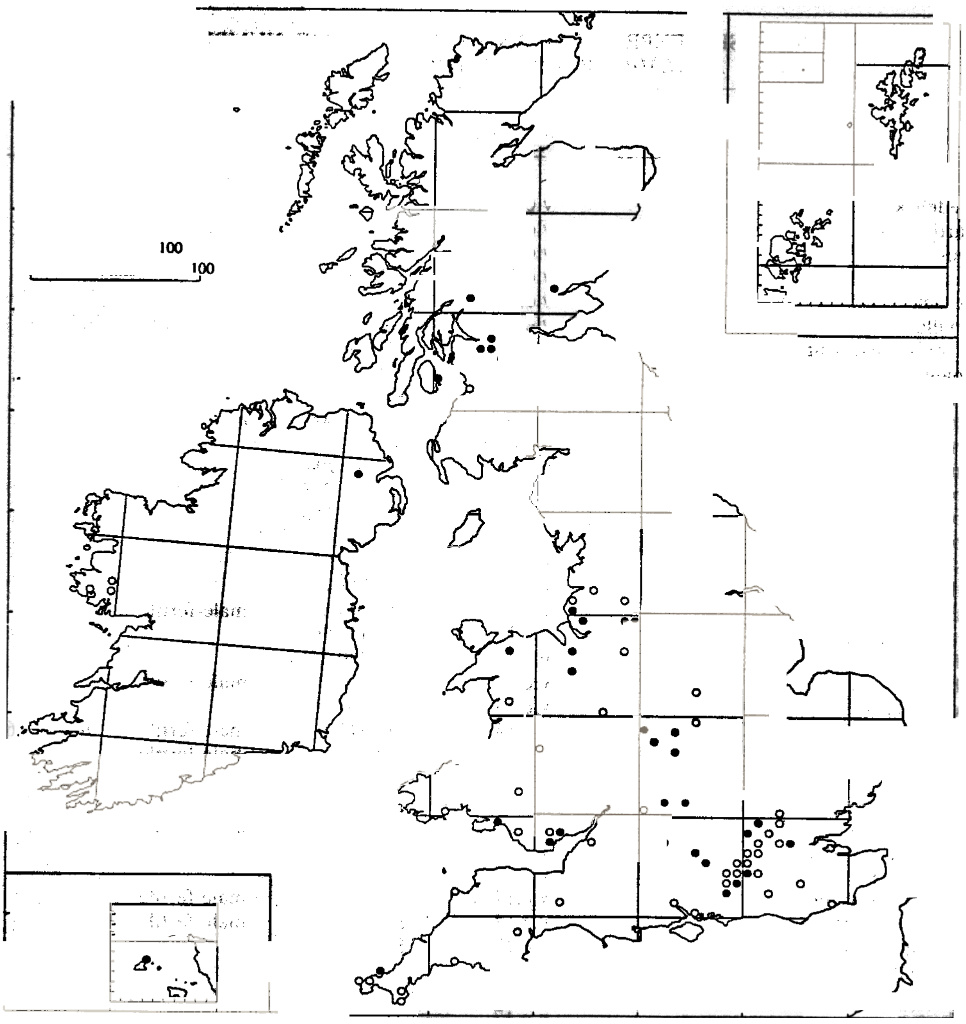

FIGURE 2. Distribution of *Fallopia* × *bohemica* in the British Isles. Open circles represent hybrids identified prior to 1993; closed circles those discovered 1993 onwards.

Cirencester Site A (Table 4), for example, a single stretch of roadside contained about 688 m^2 belonging to two different ploidy levels. Similarly, at Amroth a total length of 96 m of roadside was occupied by a single hexaploid clone. Cirencester is also distinguished in terms of the amount of genetic diversity of *F.* × *bohemica*. As male-fertile *F. sachalinensis* and the ubiquitous male-sterile *F. japonica* var. *japonica* also occur, it is possible to regard this area as something of a "hot spot" in terms of Japanese knotweed evolution, especially when the potential for back-crossing, made possible by such a concentration of genotypes, is considered.

In terms of the effectiveness of the survey, nobody sent in a record for any of the sites previously known to us. Further, the only duplication that we received in the new records was the extensive stand at Cannonhill Park, Edgbaston, of which we were notified by no fewer than three respondents. This was not a geographically based survey, and we were therefore dependent on individuals working their own particular locality; the four new records from the West Midlands, for instance, were the work of a single individual resident in the area. This fact, in combination with the

TABLE 2. LOCATION, SEX EXPRESSION AND CHROMOSOME NUMBER OF *FALLOPIA BOHEMICA* PLANTS IN THE BRITISH ISLES

Locality	Vice-county	Grid reference	Sex expression	Chromosome number
England, Wales and Scotland:				
Towednack	v.c.1	SW/43.38		2n = 66
Lanarth	v.c.1	SW/770.210	male-fertile	
St Ives	v.c.1	SW/518.403		
St Just	v.c.1	SW/361.313		
Coverack	v.c.1	SW/781.185		
Porthallow	v.c.2	SX/226.516	male-fertile	2n = 66
Trenchford reservoir	v.c.3	SX/804.824		
Philham	v.c.4	SS/259.234		
Otterford Lakes	v.c.5	ST/224.138		
Freshford, Bradford on Avon	v.c.6	ST/784.600	male-fertile	
Rownham, Bristol	v.c.6	ST/56.72		
Belmont Hill, S.W. of Bristol	v.c.6	ST/517.704		
Aldbourne	v.c.7	SU/271.753		
Aldbourne	v.c.7	SU/262.756		
Aldbourne	v.c.7	SU/253.773		
Sarisbury	v.c.11	SU/500.079		
Southampton	v.c.11	SU/395.141		
Hartley Wespall	v.c.12	SU/696.575	male-fertile	
Basingstoke, A33	v.c.12	SU/677.569		
Ashfold	v.c.13	TQ/239.286		
Midhurst	v.c.13	SU/872.208	male-fertile	
Fernhurst	v.c.13	SU/880.267		
Lye Green	v.c.14	TQ/511.336	male-fertile	2n = c. 66
Coghurst Wood, Guestling	v.c.14	TQ/830.134	male-fertile	
Camberwell New Cemetery	v.c.16	TQ/354.744	male-fertile	2n = 66
ESE Charlton Railway station	v.c.16	TQ/419.782		
Gomshall station approach	v.c.17	TQ/087.478	male-sterile	2n = 44
Haslemere, roadside	v.c.17	SU/891.332		
Critchmere, Haslemere	v.c.17	SU/882.334		
Critchmere, Haslemere	v.c.17	SU/882.337	male-fertile	
Critchmere, Haslemere	v.c.17	SU/884.342	male-fertile	
Shottermill, Haslemere	v.c.17	SU/895.339	male-fertile	
Shottermill, Haslemere	v.c.17	SU/877.330	male-sterile	
Shottermill, Haslemere	v.c.17	SU/886.340	male-fertile	
Farnham	v.c.17	SU/856.454		
Witley, Barrow Hills	v.c.17	SU/940.398	male-fertile	
Witley, N. Culmer Hanger	v.c.17	SU/943.391		
Guildford, Shalford Common	v.c.17	SU/999.470	male-fertile	2n = 44
Guildford, Wey Navigation	v.c.17	SU/998.511		
Guildford, Stringers Common	v.c.17	SU/993.526		
Guildford, canal edge	v.c.17	SU/998.511		
Guildford, Sutton Green	v.c.17	TQ/000.541		
Guildford	v.c.17	TQ/003.509		
*Winterfold, Willinghurst	v.c.17	TQ/054.424	male-sterile	
Farley Green	v.c.17	TQ/058.454		2n = 66
New Haw, Wey Navigation	v.c.17	TQ/055.620		
*Pitch Hill, nr Ewhurst	v.c.17	TQ/081.428	male-sterile	2n = 44
Abinger, B2126	v.c.17	TQ/097.464		
Holmbury Hill car park	v.c.17	TQ/099.430	male-sterile	2n = 66
Albury Heath	v.c.17	TQ/061.465		2n = 66
Near Wonersh	v.c.17	TQ/034.446		
Wisley, R.H.S. Gardens	v.c.17	TQ/066.584	male-sterile	
Weybridge	v.c.17	TQ/067.641		
Holmbury Hill, footpath to Fort	v.c.17	TQ/105.427		2n = 66

TABLE 2. *continued*

Locality	Vice-county	Grid reference	Sex expression	Chromosome number
England, Wales and Scotland:				
*Cricket ground path, Holmbury St Mary	v.c.17	TQ/109.439		
Holmbury St Mary (3 stands)	v.c.17	TQ/112.444		
Esher, river bank	v.c.17	TQ/122.627		
Burhill Golfcourse	v.c.17	TQ/104.627		
West Molesey	v.c.17	TQ/132.668		
Ham riverlands	v.c.17	TQ/165.721	male-sterile	
Cheshunt	v.c.20	TL/368.028	male-sterile	2n = 44
Northwood, Jnct. A4125	v.c.20	TQ/100.929	male-fertile	
Tottenham Marshes	v.c.21	TL/352.909	male-sterile	2n = 44
Regents Park	v.c.21	TQ/286.826		
Woolhampton, nr Newbury	v.c.22	SU/566.682		
Shipton under Wychwood, A361	v.c.23	SP/273.176	male-fertile	
Blenheim Park, Woodstock	v.c.23	SP/43.15	male-fertile	
Black Park Country Park, Wexham	v.c.24	TQ/014.832		
Cirencester, Abbey Grounds	v.c.33	SP/025.023	male-sterile	2n = 66
Cirencester, Abbey Grounds	v.c.33	SP/025.023	male-fertile	2n = 66
Cirencester, Abbey Grounds	v.c.33	SP/025.023	male-sterile	2n = 44
Cirencester, A429	v.c.33	SP/039.033	male-sterile	2n = 44
Cirencester, A429	v.c.33	SP/039.033	male-sterile	2n = c. 66
Bristol, old dockside railway	v.c.34	ST/57.72	male-fertile	
Bristol, E. of Suspension Bridge.	v.c.34	ST/565.728	male-sterile	
Bristol	v.c.34	ST/531.777	male-sterile	2n = 66
Newport	v.c.35	ST/290.853	male-fertile	
Newport	v.c.35	ST/291.854	male-fertile	
Leamington Spa, Mid. War. College	v.c.38	SP/308.656	male-fertile	
Cannon Hill Park, Edgbaston	v.c.38	SP/066.841	male-fertile	
Corley, adj. B4098	v.c.38	SP/304.845		
Cheswick Green A34/M42 Junction	v.c.38	SP/145.757	male-fertile	
Ironbridge	v.c.40	SJ/67.03	male-sterile	2n = 66
Ogmore by Sea	v.c.41	SS/87.76	male-sterile	
Whitchurch, Velindre lodge	v.c.41	ST/144.802	male-fertile	2n = 66
Whitchurch, Golf club	v.c.41	ST/154.818		
Roath	v.c.41	ST/1.7	male-fertile	
Swansea, Blackpill; NE ornate bridge	v.c.41	SS/619.907	male-fertile	
Swansea, Blackpill; rear of carpark	v.c.41	SS/619.908	male-fertile	
Swansea, Blackpill; Derwen Fawr Rd	v.c.41	SS/617.908	male-fertile	
Llandrindod Wells	v.c.43	SO/058.612	male-fertile	2n = 66
Amroth	v.c.45	SN/167.071	male-fertile	2n = 66
Pont Rhyd-sarn, Llanuwchllyn	v.c.48	SH/859.287	male-fertile	2n = c. 66
Brithdir, Caerynwch Hall	v.c.48	SH/763.177	male-fertile	2n = 66
Dolgellau, Towyn Road	v.c.48	SH/711.183	male-sterile	2n = 66
Dolgellau, riverside	v.c.48	SH/723.180	male-fertile	
Llyn Crafnant, Trefriw	v.c.49	SH/753.626		
Dee embankment	v.c.51	SJ/360.664		
Clywedog Valley, Kings Mills	v.c.50	SJ/341.489	male-fertile	
Blaby, Leicester	v.c.55	SP/577.977		
Loughborough	v.c.55	SK/544.204	male-fertile	2n = 66
Dee embankment	v.c.58	SJ/390.660		
Small Wood End, nr Sandbach	v.c.58	SJ/806.602		2n = 66
River Goyt nr Stockport	v.c.58	SJ/917.907		
River Goyt nr Stockport	v.c.58	SJ/918.906		
Ainsdale	v.c.59	SD/307.119		
Victoria Park Southport	v.c.59	SD/326.166		
Southport	v.c.59	SD/332.178	male-fertile	2n = c. 66
Ince, Backwall Lane	v.c.59	SD/330.022		

TABLE 2. *continued*

Locality	Vice-county	Grid reference	Sex expression	Chromosome number
England, Wales and Scotland:				
Liverpool, railway nr Broad Green	v.c.59	SJ/407.905		
Heaton Mersey	v.c.59	SJ/866.901		
Preston, Riversway A583	v.c.60	SD/510.298	male-fertile	2n = c. 66
0·5 km E. of South Wylam railway station	v.c.66	NZ/124.646	male-fertile	2n = 44
Ayr	v.c.75	NS/33.21		2n = 66
Johnstone; Quarrelton	v.c.76	NS/414.625	male-fertile	
Nr Bothwell	v.c.77	NS/69.59		
N. Kelvinside, Glasgow	v.c.77	NS/568.680		
Dumbrock Loch	v.c.86	NS/547.782	male-fertile	
Nr Inverarnan Bridge	v.c.87	NN/319.186		
Scone Palace grounds	v.c.89	NO/118.263		
Brodick Country Park, I. of Arran	v.c.100	NS/014.376		
Channel Isles:				
Chateau des Marais, Guernsey	v.c.S	WV/333.803		
Ireland:				
East of Recess	v.c.H16	L/90.46		2n = 66
Maam	v.c.H16	L/963.533	male-sterile	2n = 66
Roundstone	v.c.H16	L/726.424		2n = 66
Lough Neagh, Antrim	v.c.H40	J/13.86		

* denotes putative backcross

TABLE 3. BREAKDOWN OF *FALLOPIA* × *BOHEMICA* RECORDS BY SEX AND PLOIDY LEVEL
The sub-sample column records percentages of sex expression and ploidy level in the sub-sample for which these data are available; the final column expresses the same data but as a percentage of the whole sample.

Character	Number of records	Percentage of sub-sample	Percentage of total
Male-fertile	41	68·3	32·5
Male-sterile	19	31·7	15·1
2n = 44	8	22·9	6·4
2n = 66	27	77·1	21·4

very limited duplication of records experienced, suggests that a great many more hybrid localities await discovery. Where vice-county recorders happen to have an interest in the plant, as is the case in Surrey and South Lancashire, records appear to be much more numerous. In Surrey the local botanists have long been able to determine the hybrid, and had recorded it in the supplement to the county Flora (Leslie 1987). Is this abundance of records due solely to the expertise and enthusiasm of the local botanists? Does the Surrey distribution represent the sort of frequency that is waiting to be discovered in all regions, or is there something special about the history of the plants there? Without further data these questions are impossible to answer, though we do have evidence which suggests that a well-known garden designer, resident in Surrey, was recommending the planting of Japanese knotweeds and possibly had access to the hybrid.

The apparent scarcity of the hybrid in Ireland may be due to the lack of botanists looking for it there. We did not receive a single Irish response, but are informed (T. C. G. Rich, pers. comm. 1994) that the hybrid is common in parts of western Ireland.

Overall, the distribution of the hybrid (Fig. 2) bears a close resemblance to the pre-1920 distribution map for *F. japonica* var. *japonica* (Fig. 3). The significance of this, if any, is not clear. One suggestion is that the early records of establishment in some way reflect the preferred climatic conditions for the plant and that subsequent spread occurred later into sub-optimal regions; to this

TABLE 4. SEX EXPRESSION, CHROMOSOME NUMBER AND AREA OCCUPIED BY THE TWELVE STANDS OF *FALLOPIA* × *BOHEMICA* AT CIRENCESTER SITE A: ROADSIDE, A428 NEAR CIRENCESTER (V.C. 33; GR SP/039.033), 10 SEPTEMBER 1993

Code	Chromosome number	Sex expression	Area occupied (m^2)
A1	2n = 66		150
A2	hexaploid		30
A3	hexaploid		90
A4	hexaploid		24
A5	2n = 66		35
A6	hexaploid		21
A7	hexaploid		21
A8	hexaploid		114
A9	2n = 44		30
A10	hexaploid		72
A11	hexaploid		32
A12	2n = 66		69
Total area			688

TABLE 5. SEX EXPRESSION, CHROMOSOME NUMBER AND AREAS OCCUPIED BY THE ELEVEN STANDS OF *FALLOPIA* × *BOHEMICA* AT CIRENCESTER SITES C, D and E: CIRENCESTER ABBEY GROUNDS (V.C. 33; GR SP/025.023), 10 SEPTEMBER 1993

Code	Chromosome number	Sex expression	Area occupied (m^2)
C1	2n = 44		16·0
C2	2n = 66		0·5
C3	2n = 44		3·0
C4	2n = 44		1·5
C5	2n = 44		1·0
C6	hexaploid?		3·0
D1	2n = 66		60·0
D4	2n = 66		10·0
D5	2n = 66		40·0
D6			2·0
E1			100·0

day *F. japonica* var. *japonica* still has relatively few stations in East Anglia (Beerling *et al.* 1994). In the case of an introduced taxon one cannot ignore the stochastic element of where the plant happens to be first introduced. In Table 2 we have not distinguished between plants that were most probably planted and those which originated spontaneously or as throw-outs. Not only is this a virtual impossibility, since plantings for cover for game shooting (as is known to be the case with *F. sachalinensis* (D. McClintock, pers. comm.)) would be in open countryside, but, in any case, even were the plants to be in the gardens of large houses or public parks they could still act as important foci for secondary spread.

One can speculate that at early sites and at horticultural suppliers *F. japonica* was regarded as an asset, and that perhaps attempts to propagate it by seed were made. Owing to the absence of male-fertile clones of *F. japonica* var. *japonica* in this country, seed could have been produced by pollination with *F. sachalinensis* to give the hexaploid *F.* × *bohemica*. This is not to suggest that *F.* × *bohemica* can originate only through raising of seed by gardeners. There are documented cases of the spontaneous germination in situ of F_1 seed of *F.* × *bohemica* at Caerynwch Hall near Dolgellau, along with an array of hybrids that is suggestive of their having arisen unaided. However, the extreme rarity of locations where male-fertile *F. sachalinensis* grows within pollination distance of *F. japonica* var. *japonica* implies, perhaps, that this is not the main origin of *F.* × *bohemica* in the wild. At Cirencester, and possibly other locations, it is worth considering whether the hybrid is

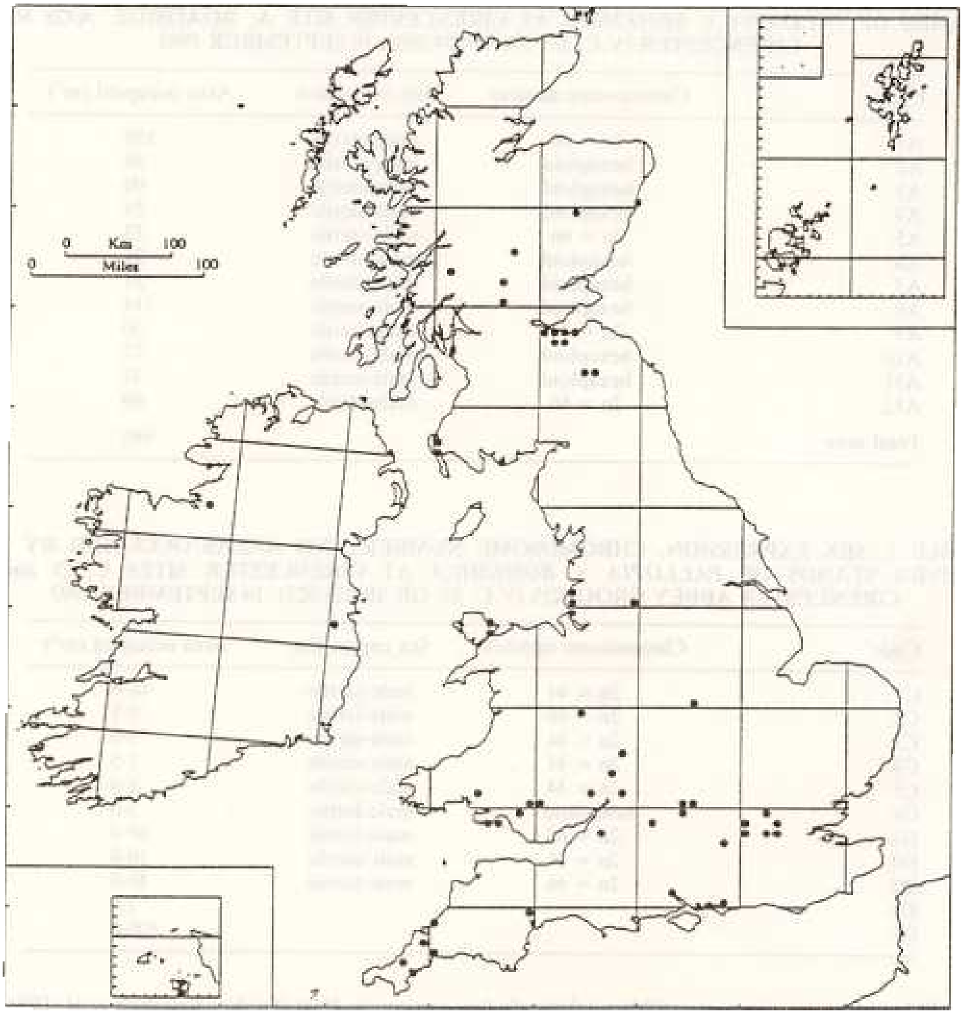

FIGURE 3. Records of *Fallopia japonica* up to 1920 (current B.R.C. records; see Conolly (1977) for additional records).

actually substituting for *F. japonica* var. *japonica*. There is more *F.* × *bohemica* present in Cirencester than of either parent. This does not imply any sort of ecological displacement, but it is possible that in some areas the first Japanese knotweed introduced was *F.* × *bohemica*.

In terms of the large excess of the hexaploid over the tetraploid hybrids, it is necessary to study the parentage of the tetraploid clones of *F. japonica* var. *compacta* × *F. sachalinensis*. In the wild, var. *compacta* is much less common than var. *japonica*, but in gardens there is a greater likelihood of finding the former, and as both sexes occur in each parent, there would appear to be even greater opportunities for hybridisation than is the case with hexaploid *F.* × *bohemica*. However, the earlier flowering time of var. *compacta* compared with *F. sachalinensis* could be a limiting factor.

One important consideration in the distribution and frequency of *F.* × *bohemica* is that, because it is frequently male-fertile, it is available as a potential pollen source for male-sterile octoploid *F. japonica*. Whilst the tetraploid hybrid has almost complete fertility, the hexaploid has irregular meiosis, low pollen viability and poor germination ability (Bailey & Stace 1991; Bailey 1994). The hexaploid is not, however, completely sterile, and there is some evidence that it can occasionally form balanced tetraploid and diploid gametes. This raises the possibility of back-crossing with one of its parents, since, were tetraploid *F.* × *bohemica* pollen grains to fertilise *F. japonica* var. *japonica* flowers, this could result in male-fertile and male-sterile octoploid plants containing at least 75% *F. japonica* var. *japonica* chromosomes and capable of replacing, to all intents and purposes, the missing male-fertile *F. japonica* var. *japonica*. Examination of the chromosome number and lower epidermal trichomes of plants grown from open-pollinated seed from male-sterile tetraploid *F.* × *bohemica* plants at Cirencester, strongly suggests that some of them had been pollinated by *F. sachalinensis*. This indicates that back-crossing can occur and might explain the origin of some of the *F. sachalinensis*-like putative tetraploids found growing in Surrey (Pitch Hill; Winterfold; Holmbury St Mary, cricket ground path: asterisked in Table 2).

In contrast to *F. japonica* var. *japonica*, which is strongly suspected of being a single vegetatively produced clone, *F.* × *bohemica* appears to have a much broader gene-pool. There must be, at an absolute minimum, four different clones in the British Isles, since male-fertile and male-sterile individuals are found at both tetraploid and hexaploid ploidy levels. Modern molecular biological techniques are available that can confirm or confound such intuitive assessments, and preliminary PCR RAPD data (Bailey *et al.* 1995) from *F. japonica* var. *japonica* accessions support the single clone theory. The application of such techniques to *F.* × *bohemica* would allow identification of the different clones and enable us to track down their putative origins and to reconstruct the history of their spread.

Currently, very little of the seed produced by Japanese knotweeds in Britain appears to germinate spontaneously, though it is worth recalling the events in the University of Leicester in 1986. The extensive collection at Leicester has a much higher proportion of male-fertile taxa than is normally found in the wild, and so pollen availability is not a problem and large amounts of seed are formed in years without early autumn frosts. In April and May 1986, some, presumably fortuitous, combination of climatic factors led to an unprecedented germination rate. Japanese knotweed seedlings were sprouting between paving stones and in cracks in the gutters, giving every impression of being the aggressive coloniser that the species must be in its native habitats on volcanic lava fields in Japan. The lesson from this is that just because recruitment from seed is not currently an important factor in the spread of hybrids or back-crosses, it cannot be ruled out; the factors responsible for the 1986 events or a change in the climate might result in a new aggressive phase in the spread of Japanese knotweeds and their hybrids.

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