

Genetic variation in Irish Whitebeam, *Sorbus hibernica* E. F. Warb. (Rosaceae) and its relationship to a *Sorbus* from the Menai Strait, North Wales

R. S. COWAN, R. J. SMITH, M. F. FAY

Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB

and

T. C. G. RICH*

*Department of Biodiversity and Systematic Biology, National Museum of Wales,
Cardiff CF10 3NP*

ABSTRACT

Genetic variation within the Irish endemic *Sorbus hibernica*, Irish Whitebeam, and its relationships to *S. aria*, *S. eminens*, *S. porrigentiformis* and a taxon from the Menai Strait have been assessed using AFLPs and morphology. *Sorbus hibernica* is genetically distinct from *S. aria*, *S. eminens* and *S. porrigentiformis* but is close to the Menai Strait taxon. *Sorbus hibernica* cannot be separated from the Menai Strait taxon using leaf or fruit characters, but they differ in ploidy.

KEYWORDS: AFLP, Ireland, *Sorbus aria*, *Sorbus eminens*, *Sorbus porrigentiformis*.

INTRODUCTION

Sorbus hibernica E. F. Warb., Irish Whitebeam, is one of the few vascular plants endemic to Ireland. It was first collected in 1885 but remained unrecognised until 1933 (Pugsley 1934), and was first described by Warburg (1952). Rich *et al.* (2005) reviewed its history, distribution and ecology, and reported that it had been recorded from at least 150 localities in 76 hectads in 29 vice-counties in Ireland. It is triploid (Bailey *et al.* 2008), and like the other polyploid members of the genus in Britain and Ireland is usually regarded as apomictic, although this has not been investigated experimentally.

Proctor & Groenhof (1992), whilst investigating *Sorbus* populations using isozymes, found similarities between *S. hibernica* and the English endemic *S. eminens* E. F. Warb., and with an unnamed taxon previously ascribed to *S. porrigentiformis* E. F. Warb. from the Menai Strait, North Wales, and suggested that this relationship should be investigated further.

Parnell & Needham (1998) found that *S. hibernica* was morphologically variable, and noted that further work was needed to confirm its apomictic nature and also to look more closely at its relationships to other taxa. In this paper, we present a DNA analysis using amplified fragment length polymorphisms (AFLP; as previously used in *Sorbus* by Fay *et al.* 2002) with some comparative morphology to follow up these suggestions.

Morphologically *S. hibernica* looks similar to *S. porrigentiformis* E. F. Warb., but it is distinct from it, and differs in having leaves with finer, uniserrate tooting and elliptic to obovate leaves (Fig. 1). Studies of plastid DNA by Chester *et al.* (2007) showed that *S. porrigentiformis* has plastid types C, D, H1, R and T, differing from *S. eminens*, *S. hibernica*, and the Menai Strait *Sorbus* which all had the plastid type A, which is also common in *S. aria* (L.) Crantz. We have therefore only included a few *S. porrigentiformis* DNA samples in the comparisons, and one sample of the related *S. 'Bristol porrigentiformis'* sensu Proctor & Groenhof (1992). Morphologically, *S. hibernica* is also easily separated from both northern and southern forms of *S. eminens* (cf. Proctor & Groenhof 1992) which have large, nearly orbicular leaves; again we have therefore only included a few DNA samples in the comparison. As *S. hibernica* is very similar in leaf shape and tooting to the Menai Strait *Sorbus*, we have both included DNA samples and carried out a more detailed morphological analysis. Some DNA samples of the diploid *S. aria* from France and England, where it is native, and from Ireland, where it is introduced (Praeger 1934), were also included for comparison.

*e-mail: tim.rich@museumwales.ac.uk

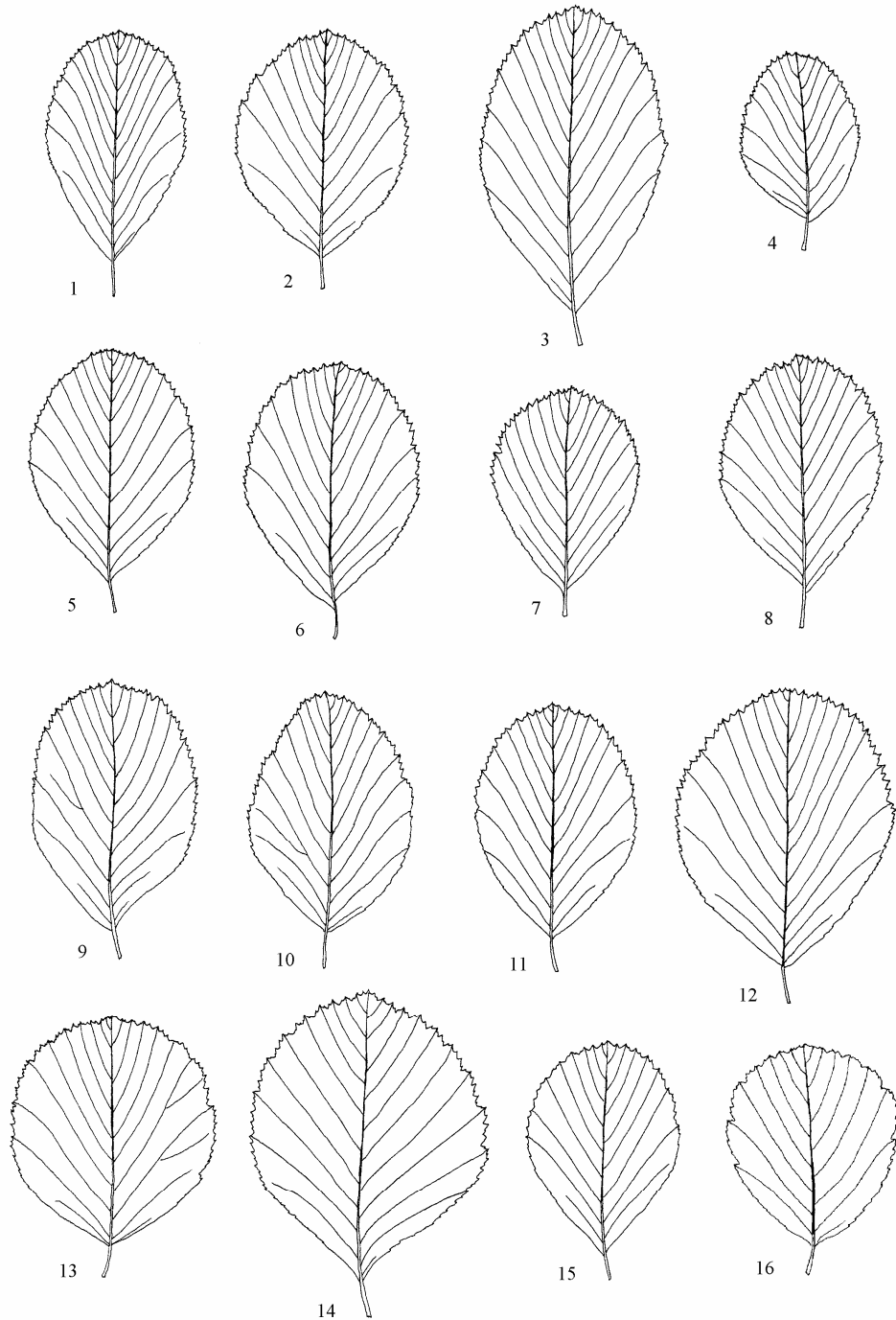


FIGURE 1. Leaves of *Sorbus* species from the short, sterile shoots. *Sorbus hibernica*: 1, Killowen. 2, Kilbeggan. 3, Clifden. 4, Cong. 5, Lough Derg. 6, Kilkenny. 7, Clonbur. 8, Cappagh. Menai Strait *Sorbus*: 9–12, Bangor. *Sorbus eminens*: 13, southern form, Shirehampton. 14, northern form, Coldwell. *Sorbus porrigentiformis*: 15, Stokeleigh. *Sorbus* 'Bristol *porrigentiformis*': 16, Leigh Woods. Not to scale.

METHODS

DNA ANALYSIS

DNA samples were collected from 21 *S. hibernica* trees across Ireland, and compared with samples of *S. aria* (seven samples), *S. eminens* (both forms, seven samples), *S. porrigentifformis* (3 samples), *S. 'Bristol porrigentifformis'* (one sample) and the *Sorbus* from the Menai Strait (3 samples). Two leaves from each tree were torn into narrow strips and put into desiccant silica gel in which they were kept until processed (Chase & Hills 1991). Voucher specimens were collected at the same time for NMW, though in some cases leaves from the typical broad, short shoots were not available due to hedge cutting or were out of reach. The samples included in the DNA analysis are listed in Table 1 with their origin, cross-referenced with the NMW accession numbers and the Kew extraction numbers. Duplicate aliquots of the DNA samples have been deposited in the Irish DNA Bank at Trinity College, Dublin.

DNA was extracted from approximately 0.2 g of dried material using a modified 2× CTAB (cetyltrimethyl-ammonium bromide) procedure (Doyle & Doyle 1987), purified and quantified using a spectrophotometer.

AFLPs were performed according to the AFLP Plant Mapping Protocol of PE Applied Biosystems Inc. (ABI). For each specimen, 0.5 µg of DNA were digested using the restriction enzymes MseI and EcoRI. Standard adaptors (PE Applied Biosystems) were ligated to the genomic digests. Twenty four unique primer combinations were screened for their ability to amplify scoreable bands, from which two were selected for this study. Amplification fragments were separated on an ABI 3100 DNA analyser. Genescan 3.7 and Genotyper 2.0 were used to analyse the fragments which were scored as either present (1) or absent (0) for all individuals. The resulting binary matrix was analysed using the UPGMA (Unweighted Pair-Group Method using Arithmetic Averages) algorithm in the software package PAUP version 4.0d64 for Macintosh (Swofford 1998) and by Principal Co-ordinates Analysis (PCOA) in the R Package for Multivariate Analysis version 4.0 (Casgrain & Legendre 1999) using Jaccard's coefficient.

MORPHOLOGY

Broad leaves from the short vegetative shoots, excluding the oldest and youngest leaf (Aas *et al.* 1994), were measured on 88 leaves of

S. hibernica, 50 leaves of *S. aria* from Ireland and 56 leaves of the Menai Strait *Sorbus* on herbarium material in the Welsh National Herbarium (NMW), Trinity College Dublin (TCD) and Belfast (BEL). As many as possible of the trees sampled during the DNA analysis were included, but some lacked the short shoots or were poor specimens. The samples used additional to the DNA analysis samples are given in Appendix 1.

The leaf length (excluding petiole), width, distance along the mid-vein of the widest point, the angle of veins to the midrib at the middle of the leaf, and the total number of veins were measured. From these, the leaf length:width ratio and the position of the widest point along the leaf (expressed as a percentage) were derived. The seven characters were then analysed using Principal Components Analysis (PCA) with a correlation matrix in PAST version 1.72 (Hammer *et al.* 2001).

RESULTS

DNA ANALYSIS

A total of 187 size fragments were scored of which 95% were polymorphic (10 invariable). In the UPGMA analysis (Fig. 2), the *Sorbus hibernica* samples, Group A, all cluster together and separately from all other taxa. This is a relatively genetically uniform group which represents the main *S. hibernica* taxon with elliptic-obovate leaves and fine, uniserrate toothings. The relatively tight grouping suggests it is probably (predominantly at least) apomictic but that cannot be confirmed from these data.

The three Menai Strait samples, Group B, form a group distinct from, but obviously close to, *S. hibernica*. Group C contains the group of apomictic polyploid taxa from south-west England, the two forms of *S. eminens* and the form of *S. porrigentifformis* from Bristol; these are clearly closely related to each other and are approximately genetically equidistant from the *S. hibernica* group and the Menai Strait samples. The three British *S. porrigentifformis* samples, Group E, form a distinct group that is genetically more distant from these groups than *S. aria* from France and Ireland.

The samples of the genetically diverse sexual diploid *S. aria* group by geographic origin. One Group D *S. aria* specimen was collected at Ballynahinch, Galway (vc. H16), the type locality of *S. hibernica* (Warburg 1957), where we failed to refind *S. hibernica*.

TABLE 1. *SORBUS* SAMPLES ANALYSED DURING DNA ANALYSIS.
SOME *S. HIBERNICA*, *S. ARIA* AND *S. 'MENAI STRAIT'* SAMPLES WERE
ALSO USED FOR THE LEAF MORPHOLOGICAL ANALYSIS

Taxon	Locality	Vice-county/Region	Country	Voucher	Kew DNA bank no.
<i>S. 'Bristol porrigentiformis'</i>	Leigh Woods	6 North Somerset	England	2001.25.273	36.80
<i>S. 'Menai Strait'</i>	Menai Strait	49 Caernarfonshire	Wales	2002.17.68	42.12
<i>S. 'Menai Strait'</i>	Menai Strait	49 Caernarfonshire	Wales	2002.17.66	42.13
<i>S. 'Menai Strait'</i>	Menai Strait	49 Caernarfonshire	Wales	2002.17.67	42.15
<i>S. aria</i>	Above Senanque	Provence	France	Civeyrel <i>et al.</i> 492, K	46.30
<i>S. aria</i>	Ballynahinch	H16 West Galway	Ireland	2003.20.26	51.01
<i>S. aria</i>	Burnham Beeches	24 Buckinghamshire	England	2001.48.10	24.10
<i>S. aria</i>	Burnham Beeches	24 Buckinghamshire	England	2001.49.11	27.20
<i>S. aria</i>	Lecarrow	H25 Roscommon	Ireland	2003.4.1042	49.03
<i>S. aria</i>	Roundstone	W16 West Galway	Ireland	2003.20.24	50.05
<i>S. aria</i>	Tallyho	H23 Westmeath	Ireland	2003.20.30	49.06
<i>S. eminens</i> , southern form	Cheddar Gorge	6 North Somerset	England	2001.25.141	36.05
<i>S. eminens</i> , southern form	Cheddar Gorge	6 North Somerset	England	2001.25.145	36.12
<i>S. eminens</i> , southern form	Cheddar Gorge	6 North Somerset	England	2001.25.142	36.16
<i>S. eminens</i> , southern form	Cheddar Gorge	6 North Somerset	England	2001.25.144	38.05
<i>S. eminens</i> , southern form	Leigh Woods	6 North Somerset	England	2001.25.274	36.15
<i>S. eminens</i> , northern form	Seven Sisters	36 Herefordshire	England	2001.25.51	38.20
<i>S. eminens</i> , northern form	Symonds Yat	34 West Gloucestershire	England	2001.25.219	38.10
<i>S. hibernica</i>	Ballybetagh	H21 Dublin	Ireland	2001.25.289	41.12
<i>S. hibernica</i>	Ballybetagh	H21 Dublin	Ireland	2003.4.1048	51.02
<i>S. hibernica</i>	Ballybetagh	H21 Dublin	Ireland	2003.4.1045	51.03
<i>S. hibernica</i>	Ballybetagh	H21 Dublin	Ireland	2003.4.1046	51.08
<i>S. hibernica</i>	Ballybetagh	H21 Dublin	Ireland	2003.4.1049	52.01
<i>S. hibernica</i>	Ballybetagh	H21 Dublin	Ireland	2003.4.1047	52.02
<i>S. hibernica</i>	Cappagh	H8 Limerick	Ireland	2003.4.1055	52.03
<i>S. hibernica</i>	Clifden	W16 West Galway	Ireland	2003.20.25	50.06
<i>S. hibernica</i>	Dalkey Hill	H21 Dublin	Ireland	2003.4.1050	51.04
<i>S. hibernica</i>	Dalkey Hill	H21 Dublin	Ireland	2003.4.1051	51.06
<i>S. hibernica</i>	Dalkey Hill	H21 Dublin	Ireland	2003.4.1052	51.07
<i>S. hibernica</i>	Dalkey Quarry	H21 Dublin	Ireland	2003.4.1054	51.05
<i>S. hibernica</i>	Drumnasole	H39 Antrim	Ireland	2002.27.46	42.03
<i>S. hibernica</i>	Kilbeggan	H23 Westmeath	Ireland	2003.20.29b	49.04
<i>S. hibernica</i>	Kilbeggan	H23 Westmeath	Ireland	2003.20.29c	49.05
<i>S. hibernica</i>	Kilbeggan	H23 Westmeath	Ireland	2003.20.29	50.08
<i>S. hibernica</i>	Kilcullen Upper	H6 Waterford	Ireland	2003.20.9	49.07
<i>S. hibernica</i>	Lecarrow	H25 Roscommon	Ireland	2003.4.1043	49.02
<i>S. hibernica</i>	Lough Derg	H10 North Tipperary	Ireland	2003.20.12	50.03
<i>S. hibernica</i>	Lough Derg	H10 North Tipperary	Ireland	2003.20.13	50.04
<i>S. hibernica</i>	Priesthaggard	H12 Wexford	Ireland	2003.20.5	49.08
<i>S. hibernica</i>	Seagull Bog	H18 Offaly	Ireland	2003.20.32	50.07
<i>S. porrigentiformis</i>	Ban-y-Gor	34 West Gloucestershire	England	2002.17.105	27.90
<i>S. porrigentiformis</i>	Craig-y-cilau	42 Brecknockshire	Wales	2002.17.42	25.60
<i>S. porrigentiformis</i>	Cwm Clydagh	42 Brecknockshire	Wales	2001.25.74	21.80

¹All NMW except one sample of *S. aria* from France for which the voucher is held at K

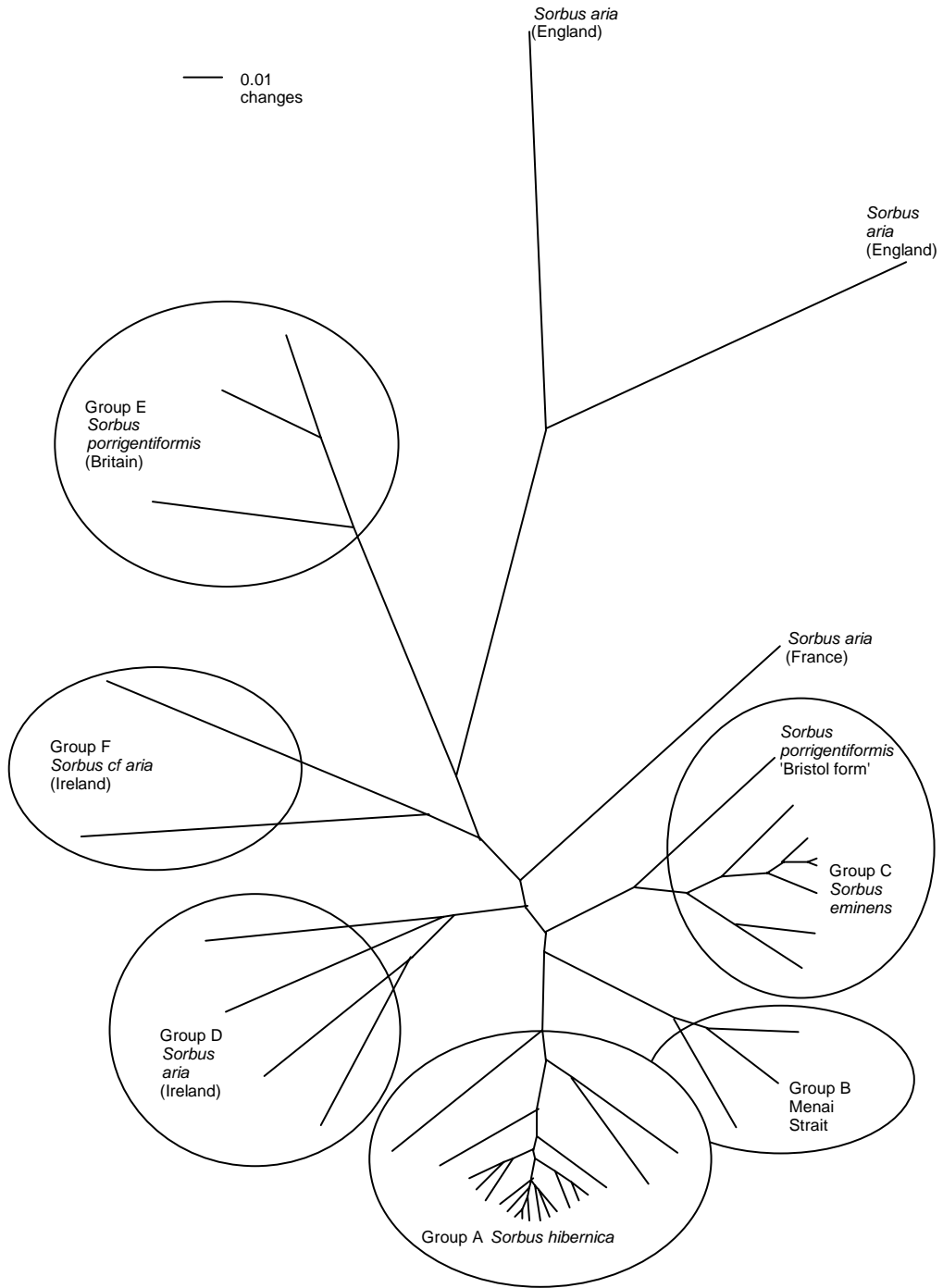


FIGURE 2. Unrooted UPGMA dendrogram showing relationship between the *Sorbus* DNA samples studied using amplified fragment length polymorphisms. The origins of the samples are listed in Table 1.

Two samples labelled *S. cf aria*, Group F, look intermediate between *S. hibernica* and *S. aria* and require further study. Tree 49.02 from Lecarrow, Roscommon (v.c. H25) is from a mixed population with clear *S. aria* (tree 49.03) and also *S. hibernica* (fruit sample NMW; no DNA sample). Tree 49.08 is from Priesthaggard, Wexford (v.c. H12), an area where some *S. hibernica* is certainly present but *S. aria* is unknown.

In the DNA Principal Co-ordinates Analysis (Fig. 3) based on the same data as Figure 2, axis one accounts for 24% of the variance and axis two for 15%. The clustering shows a very similar pattern to that found in the UPGMA analysis. There is clear separation of *S. porrigentiformis* and both forms of *S. eminens* from the other taxa and each other, the *S.* 'Bristol

porrigentiformis' clustering with *S. eminens*. The Menai Strait taxon (Group B of Fig. 2) is close to but separated from *S. hibernica*. *Sorbus aria* is separated from *S. hibernica*, and the two *S. cf aria* samples (Group F of Fig. 2) are outliers near *S. aria* and *S. hibernica*.

MORPHOLOGY

In the morphological Principal Components Analysis (Fig. 4), axis one accounts for 40% of the variance and axis two for 22%. There is reasonable separation between *S. aria*, which is mostly confined to the upper right corner of the graph (a few more widely scattered samples elsewhere), and *S. hibernica* and the Menai Strait *Sorbus* in the lower, left hand corner of the graph. There is complete overlap between *S. hibernica* and the Menai Strait *Sorbus* and they cannot be distinguished morphologically

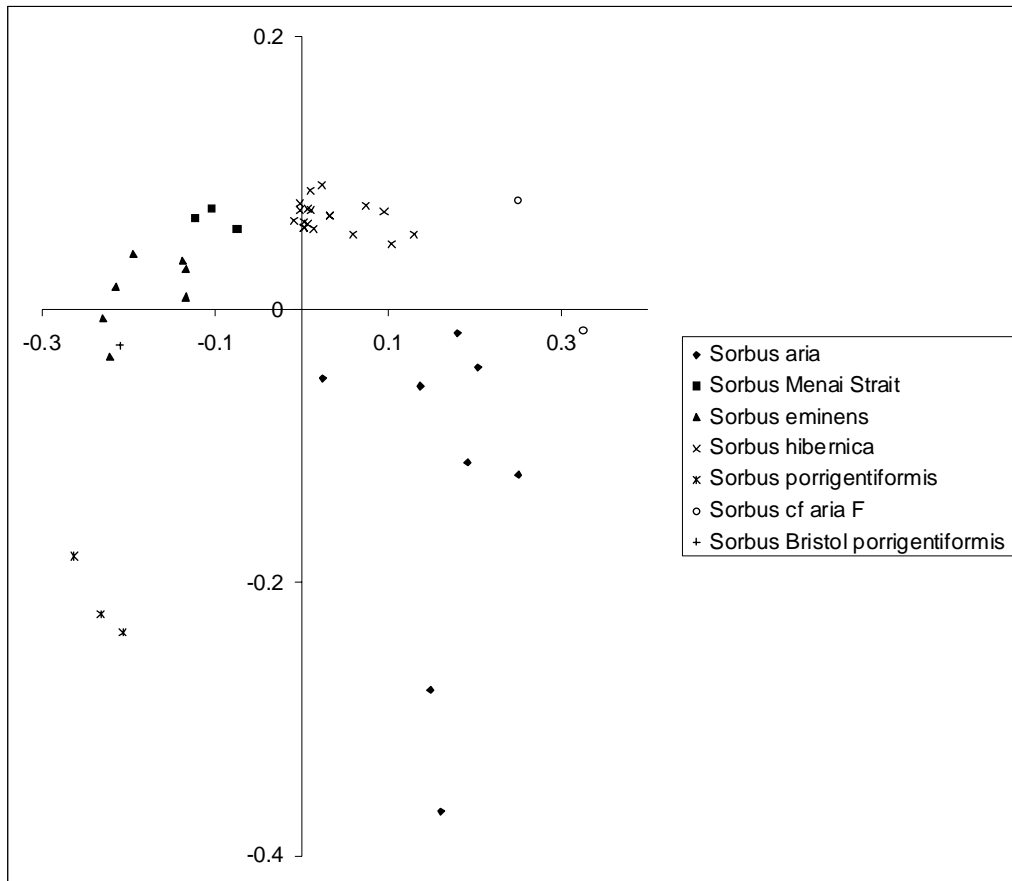


FIGURE 3. Principal Co-ordinates Analysis plot of *Sorbus* taxa based on amplified fragment length polymorphisms. The origins of the samples are listed in Table 1, and are the same as in Figure 2.

(see also Fig. 1). The *S. hibernica* plants of Groups B, C and D, and the proposed intermediate plants of Group F (cf. Fig. 2) mostly fall near the centre of the plot clustering within *S. hibernica* and do not form discrete groups.

DISCUSSION

The DNA analysis shows that *S. hibernica* is distinct from *S. aria*, *S. eminens* and *S. porrigentiformis* but is close to the Menai Strait taxon. In agreement with Proctor & Groenhof (1992), the Menai Strait taxon is also confirmed to be genetically distinct from *S. porrigentiformis* in which it was formerly included. The morphological data confirm that *S. hibernica* is distinct from *S. aria* (as also found by Parnell & Needham 1998), but not from the Menai Strait *Sorbus*.

The limited genetic variation found in *S. hibernica* suggests it is probably apomictic, like most *Sorbus* microspecies. To judge from the AFLP data here, *S. hibernica* is less genetically variable than the sexual diploid *S. aria*. Nonetheless, there is some genetic variation in *S. hibernica*, as has been observed for other apomictic polyploids in other groups (e.g. *Hieracium*, Chapman *et al.* 2003; Rich *et al.* 2008). There is no geographic pattern to the genetic variation observed. This variation in *S. hibernica* is probably caused by random mutations; Bengtsson (2003) showed that mutations can slowly accumulate in species with asexual breeding systems leading to variable populations which show little genetic structure. The variation could also be caused by hybridisation, sub-sexual reproduction, or repeated derivation from its parents. Although

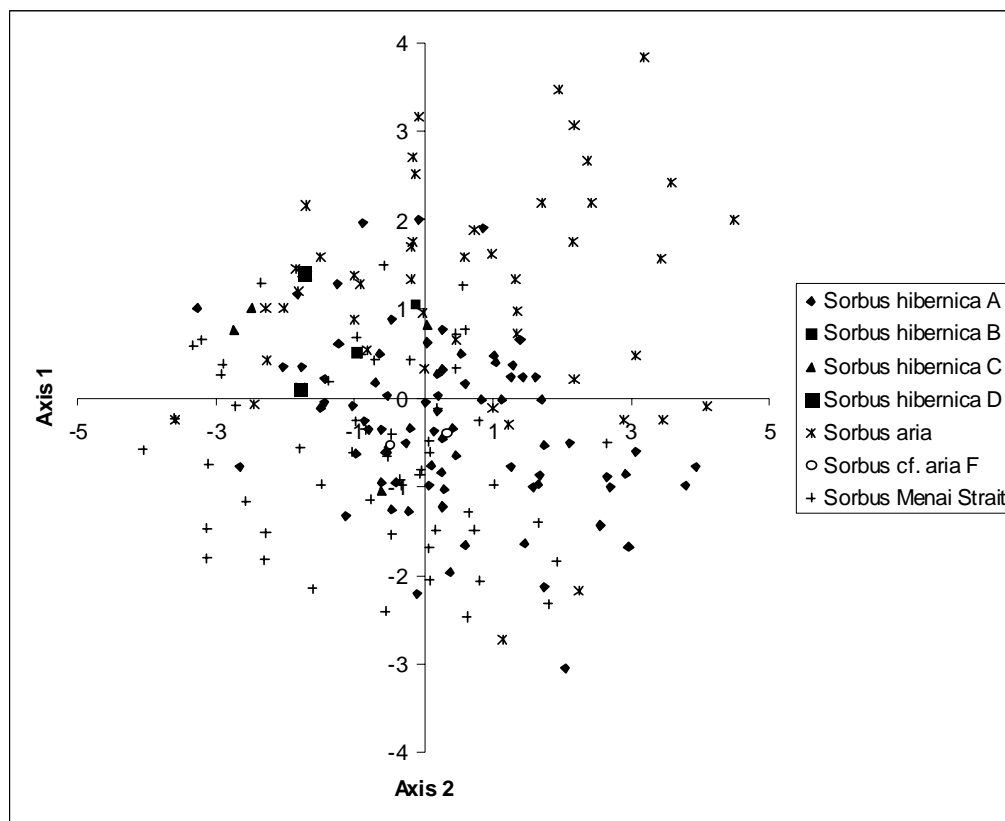


FIGURE 4. Principal Components Analysis plot of leaf characters in *Sorbus*. The group labels relate to the same groups shown in Figure 2, although not all samples are represented as some voucher specimens were inadequate for morphological analysis; other samples used are listed in Appendix 1.

the possibility of hybrids between *S. aria* and *S. hibernica* has been proposed here, there is no clear evidence to demonstrate that this occurs, and such plants might be expected to be morphologically significantly different from *S. hibernica*. Significant sub-sexual reproduction is also unlikely in a triploid. The origin of *S. hibernica* is currently unknown, but it is likely to result from *S. aria* crossing with a tetraploid such as *S. eminens*, *S. porrigentiformis* or *S. rupicola* (Syme) Hedl. in Britain where all the taxa occur, with subsequent dispersal by birds migrating to Ireland (Wernham *et al.* 2002). *Sorbus hibernica* is also not as uniform morphologically as some of the other apomictic taxa we have studied (e.g. *S. bristoliensis*; Houston *et al.* 2008); Parnell & Needham (1998) also found that it was variable.

Although the Menai Strait plants form a distinct genetic group, they are clearly closely related to *S. hibernica*. Their minor genetic separation could result from long-term isolation across the Irish Sea, or could reflect a similar origin. They differ in chromosome number as the Menai Strait plants are reported

as tetraploid and *S. hibernica* as triploid (Bailey *et al.* 2008), suggesting they have different origins. Morphologically, the two taxa cannot be distinguished from the leaves (Figs 1 and 4), and the limited data on fruit size, shape and colouration available show strong overlap between *S. hibernica* and the Menai Strait *Sorbus* (Proctor & Groenhof 1992; pers. obs. T. Rich). Further morphological characters will need to be sought to separate the Menai Strait *Sorbus* from *S. hibernica*.

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APPENDIX 1. *SORBUS* SAMPLES USED IN MORPHOLOGICAL ANALYSIS*SORBUS ARIA*

Loch Bunny, H9 Clare, 19 July 1978, D. A. Webb (**TCD**). Ardrahey, H15 SE Galway, 21 August 1952, D. A. Webb (**TCD**). Ballinadareen, H15 SE Galway, 19 July 1978, D. A. Webb (**TCD**). Gort, H15 SE Galway, 20 August 1952, T. G. Tutin (**TCD**). Oranmore, H15 SE Galway, 19 July 1978, D. A. Webb (**TCD**). Oughterrard, H15 SE Galway, 1978, D. A. Webb (**TCD**). Ballynahinch, H16 W Galway, 21 September 2003, L. Houston (**NMW**). Clontarf golf course, H21 Dublin, 29 September 1978, P. H. Pitkin & D. A. Webb (**TCD**). Portlick Castle, H23 Westmeath, 16 August 1982, D. L. Kelly (**TCD**). Tallyho, H23 Westmeath, 23 September 2003, L. Houston (**NMW**). Whitehill, Castlepollard H23 Westmeath, 8 June 1983, D. A. Webb & F. H. Perring (**TCD**). Slish Wood, H28 Co Sligo, 1962, D. E. de Vasian (**BEL**). Lower Kilycolpy, H36 Tyrone, 29 July 1927 and 10 September 1937, F. H. W. Kerr (**BEL**). Carngaver, 8 August 1986, J. Harron (**BEL**).

SORBUS HIBERNICA (ADDITIONAL TO SPECIMENS LISTED IN TABLE 1)

Boolabrien Upper, H6 Co Waterford, 18 September 2003, L. Houston (**NMW**). Coolbunna, H6 Co Waterford, 10 June 2003, P. R. Green (**NMW**). Ballyallia Lough, H9 Clare, C. M. Brady, 22 June 2002 (**NMW**). Lough Derg, H10 North Tipperary, 18 September 2003, L. Houston (**NMW**). Loughmerans, H11 Co Kilkenny, 29 September 2006, T. C. G. Rich, R. N. Goodwillie & D. A. Cann (**NMW**). Pilltown, H12 Co Wexford, 11 August 1958, D. A. Webb (**TCD**). Priesthaggard, H12 Co Wexford, 17 September 2003, L. Houston (**NMW**). Gort, west of, H15 SE Galway, 20 August 1952, T. G. Tutin (**TCD**). Clifden, H16 West Galway, 10 June 1990, T. G. Evans (**NMW**). Errislannan Peninsula, H16 West Galway, 5 September 1979, D. A. Webb (**TCD**). Cong, H17 NE Galway, 30 August 2005, D. T. Price (**NMW**). Tullamore, H18 Offaly, 1978, D. A. Webb (**TCD**). Between Greenane and Rathdrum, H20 Co Wicklow, 11 September 1978, D. A. Webb (**TCD**). Ballybetagh, H21 Co. Dublin, 25 September 2004, P. H. Carvill (**NMW**). Killowen, 25 September 2006, T. C. G. Rich & D. A. Cann (**NMW**). Loch Fea, H36 Tyrone, 28 September 2006, T. C. G. Rich & D. A. Cann (**NMW**). Inishmaine, H26 East Mayo, 30 August 2005, D. T. Price (**NMW**). Clonbur, H26 East Mayo, 30 August 2005, D. T. Price (**NMW**).

SORBUS 'MENAI STRAIT'

Menai Strait, 19 September 1985, T. C. G. Rich (**NMW**). Menai Strait, 21 August 1989, G. Hutchinson (**NMW**). Nant Porth, 12 June 1990, M. C. F. Proctor (**NMW**). Menai Strait, 9 July 2002, T. C. G. Rich & R. A. Jones (**NMW**). Upper Bangor, 19 September 2003, T. Dines & W. McCarthy (**NMW**).