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Populations sizes and leaf morphology of the Welsh endemics *Sorbus cambrensis* Welsh Whitebeam and *Sorbus stenophylla* Llanthony Whitebeam (Rosaceae)

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Abstract
The distribution and population sizes of *Sorbus cambrensis* (Welsh Whitebeam) and *S. stenophylla* (Llanthony Whitebeam) (Rosaceae) are revised based on field surveys. About 224 trees of *S. cambrensis* occur in eight populations/subpopulations (including in the Llanthony Valley), and about 96 trees of *S. stenophylla* occur in five populations/subpopulations. Morphological analysis of leaves confirmed the two species were different and showed some variation within each species.

Keywords: Endangered, IUCN threat status, Wales, principal component analysis

Introduction

Sorbus cambrensis M. Proctor (Welsh Whitebeam) and *S. stenophylla* M. Proctor (Llanthony Whitebeam) (Rosaceae) were first described as part of the *S. porrigentiformis* group (Rich & Proctor, 2009; Rich *et al.,* 2010). Both species were subsequently found to be unusual in being pentaploid (Pellicer *et al.,* 2012).

Summaries of the distributions given by Rich & Proctor (2009) and Rich *et al.,* (2010) indicated that both whitebeams were rare Welsh endemics of the eastern Brecon Beacons (v.c.35 Monmouthshire and v.c.42 Brecon), though it was noted that further studies were needed of populations at Craig y Cilau and Pwll-du Quarry, Govilon. In autumn 2012, Martin Lepší undertook these studies as part of collaborative work during his PhD research. Morphological studies of leaves were undertaken to look at differentiation between, and within, each species, and data on population sizes were collected. The aim of this paper is to present the results of the studies.

Methods

Field surveys at all known sites were carried out in 2012 by M. Lepší, with a few minor 2014 updates by T. Rich. Additional sites in the Llanthony Valley were also searched by M. Lepší resulting in discovery of some unknown populations. Each site was searched as far as practicable (as most trees were on cliffs), and the locations of plants mapped. Population counts for *S. cambrensis* at Craig y Cilau in 2002 (Rich, 2003, as 'largeleaved *S. porrigentiformis*') were used to avoid redoing a full census of this large and complex site.

Multivariate morphometric analyses were used to evaluate variability of *Sorbus cambrensis* and *S. stenophylla* and reveal species-specific characters. Five well-developed, mature, intact leaves from the middle part of short sterile shoots were collected for morphological analysis per individual. Five or six individuals were sampled at each of nine populations (six of S. *cambrensis* and three of *S. stenophylla*) giving a total of 53 trees sampled. All trees sampled for morphometric analysis were tested for pentaploid level by flow cytometry (courtesy J. Pellicer). 2012 was a poor fruiting year so data on fruit were not collected.

The leaves were carefully flattened and dried, scanned at 300 dpi and scored for 15 leaf characters using tpsDig software (Rohlf, 2006). The character set was chosen on the basis of published keys, floras and taxonomic studies for *Sorbus* (e.g. Kutzelnigg, 1995; Meyer *et al.*, 2005; Rich *et al.*, 2010; Lepší *et al.*, 2015):

1. AB - angle of lamina base.
2. AI - angle of incision between 3rd and 4th lobe.
3. AT - angle of leaf apex.
4. AT2 - angle of terminal tooth of 3rd lobe.
5. AV - angle of third lateral vein from the leaf base to the midrib.
6. I - depth of incision between 3nd and 4rd lateral vein from laminar base.
7. L - width of 4th lobe.
8. LL -lamina length.
9. LL:LW - leaf length to leaf width ratio.
10. LW - lamina width.
11. NT1 - number of teeth at 4th lobe.
12. NT2 - number of single teeth on the leaf apex.
13. NV - number of lateral lamina veins.
14. P - petiole length.
15. WP - widest point from leaf base.

Five measurements of each character per individual were recorded and their arithmetic mean was used as the value for each individual in all morphometric analyses. Non-parametric Pearson correlation coefficients were calculated for pairs of characters of each species and for the whole dataset to reveal relationships among characters. Principal component analyses (PCA) were performed to give an insight into the overall pattern of morphological variation and to reveal intraspecific variability and potential separation of the two species. Prior to the PCA, the data were log-transformed and standardized to have a zero mean and unit standard deviation so that the characters were on a comparable scale and had the same weight in analyses. Linear Discrimination Analyses (LDA), which maximize differences between a priori defined groups, were used to test the discriminating power of morphometric characters, following the method described by Lepš & Šmilauer (2003) using forward selection of characters with non-parametric Monte Carlo permutation tests (999 permutations; only axes with P level

<0.05 were considered). A cross-validated classificatory Linear Discriminant Analysis based on probabilities using only characters selected as discriminating variables by the previous analysis was performed in R version 2.12.2 (R Development Core Team, 2011) using the "lda" function in the MASS package (Venables & Ripley, 2002). PCA and LDA were carried out using CANOCO (Lepš & Šmilauer, 2003).

The method of elliptic Fourier approximation (Kuhl & Giardina, 1982) incorporated in the SHAPE 1.2 software package (Iwata & Ukai, 2002) was used to summarise the variation in leaf shapes.

Results

Population sizes

The distributions of both species are shown in Fig. 1. About 224 trees of *S. cambrensis* were found in eight populations/subpopulations (Table 1), and about 96 trees of *S. stenophylla* in five populations/subpopulations (Table 2).

All records from the Llanthony Valley were attributed to *S. stenophylla* by Rich *et al.,* (2010) on the basis that *S. cambrensis* was not recorded there, partly on the advice of M.C.F. Proctor after discussing some puzzling herbarium material with him in 2007-2008 prior to submission of Rich & Proctor (2009) in which both species were named. As it is now established that both *S. stenophylla* and *S. cambrensis* do occur in the Llanthony Valley, the localities are briefly reviewed below, together with some of the cytology data. The localities are ordered from south to north (Fig. 1).

1 Pwll-du Quarry, Govilon v.c.35

A small population occurs on the wooded natural crags and quarry edge crags and is now confirmed as *S. stenophylla*. One young tetraploid *S. porrigentiformis* plant also occurs here, with *S. anglica* in the quarry. The ploidy level of another tree nearby at the Tumbles SO25561148 collected by D. Green on 14/10/2011 requires verification.

2 Cwm Clydach (including Blackrock and Llanelly Hill) v.c.42

This is the type locality of *S. cambrensis*, where it occurs on open cliffs, on rocks in woodland, in grassland and even on field banks, with occasional *S. anglica*. Most trees occur in the Cwm Clydach National Nature Reserve with a few scattered nearby which seem best treated as one population. Some trees by the A465 may have been lost to the 2017-2021 roadworks.

A tetraploid chromosome count of a *S. porrigentiformis* group plant from Cwm Clydach was reported by Q.O.N. Kay (Proctor & Groenhof, 1992; Bailey *et al.*, 2008) whereas our seven flow cytometry counts including the type tree were pentaploid (Pellicer *et al.*, 2012, and unpublished 2012 data); no members of the *S. porrigentiformis* group other than *S. cambrensis* are currently known here.

3 Coed Pantydarren v.c.42

The roadside quarry and the rocks above hold a uniform population of *S. cambrensis*, with some large old trees. The locality name is also cited as Darren Disgwlyfa based on the 1:50,000 Ordnance Survey maps, but the 1:25,000 maps indicate the locality at

SO219138 is better cited as Coed Pantydarren than Darren Disgwlyfa, which has a small quarry at SO219143 that holds no whitebeams.

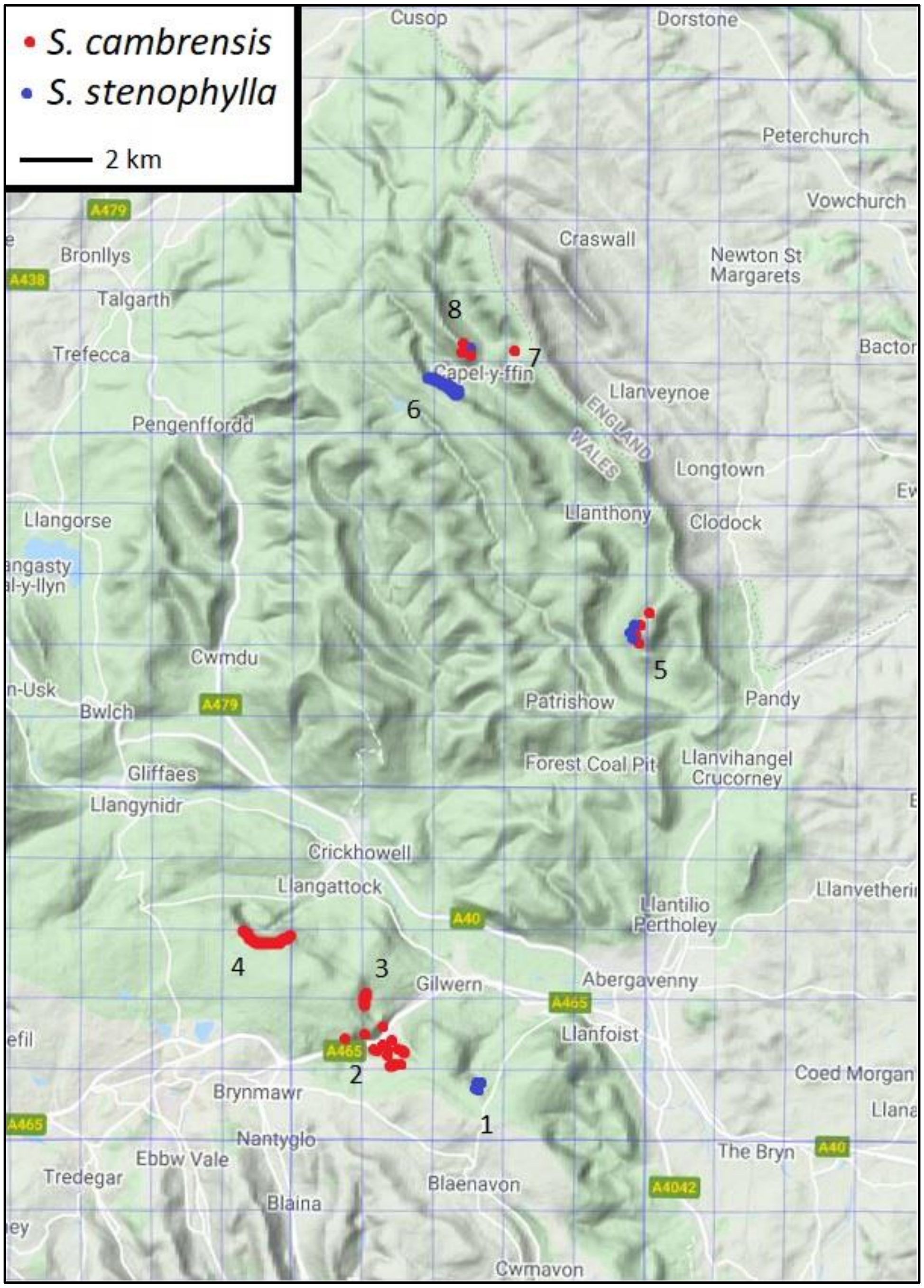

Figure 1. *Sorbus cambrensis* (red) and *S. stenophylla* (blue) localities. 1 Pwll-du Quarry, Govilon. 2 Cwm Clydach. 3 Coed Pantydarren. 4 Craig y Cilau. 5 Darren, Cwmyoy. 6 Tarren yr Esgob. 7 Capel-y-ffin. 8 Darren Lwyd.

Table 1. Distribution and population sizes of *Sorbus cambrensis.*

Locality	v.c.	Grid reference	Date(s)	Population size
1a Cwm Clydach NNR to Llanelly Hill	42	SO2220 to SO220119	6 & 16/9/2012 and/9/2014	43 trees
1b Blackrock	42	SO212125	9/2014	1 tree
3 Coed Pantydarren	42	SO219138	6 & 18/9/2012	*c.*20 trees
4 Craig y Cilau	42	SO1815 and SO1915	9/2002	67 trees with many other *Sorbus* species (Rich 2003)
5a Darren, Cwmyoy	35	SO2924	9 & 13/9/2012	*c.*50 trees accessed from below
5b Weild, Cwmyoy	35	SO302253	19/9/2012	3 trees
7 Capel-y-ffin, NNE of	42	SO259320	28/9/2012	*c.*20 trees
8 Darren Lwyd	42	SO243330	8/9/2012	*c.*20 trees

Table 2. Distribution and population sizes of *Sorbus stenophylla.*

Locality	v.c.	Grid reference	Date(s)	Population size
1 Pwll-du quarry, Govilon	35	SO2511	9/2014	16 trees
4 Darren, Cwmyoy	35	SO2924	9 & 13/9/2012	5 trees
6a Tarren yr Esgob southern cwm	35/ 42	SO252306	8/9/2012 & 21/9/2014	*c.*50 trees on rocks
6b Tarren yr Esgob, main slopes	42	SO2331	8/9/2012 & 21/9/2014	*c.*20 trees on rocks in woodland and 4 on top crags
8 Darren Lwyd	42	SO243330	8/9/2012	1 tree with possible juveniles

4 Craig y Cilau v.c.42
Sorbus cambrensis is scattered on the main central cliffs within the National Nature Reserve. Tetraploid *S. porrigentiformis* trees and triploid *S. porrigentiformis* group trees also occur here often mixed with *S. cambrensis* and other taxa.

Rich *et al.,* (2010) cited some plants at Craig y Cilau that matched *S. stenophylla* in morphology but required verification; we have not refound any *S. stenophylla* and such plants may be poorly-grown *S. cambrensis* or possibly small *S. leptophylla*.

5 Darren, Cwmyoy v.c.35
Sorbus cambrensis is locally frequent along the top edge of the cliff (with two plants of the unnamed triploid subgenus *Tormaria* plant; Rich *et al.,* 2014) where they are tolerably safe to access, with a discrete subpopulation on the crags just to the north above Weild. *S. stenophylla* is much less frequent on the lower rocks and was very difficult to access safely.

6 Tarren yr Esgob v.c.35/v.c.42
This is the type locality of *S. stenophylla* and is the only whitebeam at this site. *S. stenophylla* occurs mainly on the central crags with most plants on the lower rocks and a few bushes on the top ridge. Most plants are in v.c.42 Breconshire but some occur in v.c.35 Monmouthshire though it is not always certain that the vice-county boundary has been correctly applied in the past. We have included records for Pen-y-Wyrlod and Maes-y-Ffin.

7 Capel-y-ffin v.c.42
This small population of *S. cambrensis* east of the village was first found by M. Lepsi in 2012 and has some trees to 10 m tall.

8 Darren Lwyd v.c.42
The trees on the steep NE-facing cliffs at the southern end at SO243330 are *S. cambrensis* with one possible *S. stenophylla*, but are mostly poorly developed and also difficult to access. All trees here have been previously attributed to *S. stenophylla* alone. We have not refound trees on the gentler slopes *c.*800 m to the north at *c.*SO240340 where they were reported in the 1970s.

Multivariate morphometric analyses
Univariate statistics of quantitative characters are summarized in Table 3.

The PCA showed *S. cambrensis* and *S. stenophylla* were morphologically distinct (Figs. 2, 3). The strongest contribution to the morphological distinctiveness of both species (i.e. the most strongly correlated characters with the first component axis) were the ratio length of lamina/width of lamina (LL:LW), the angle of incision between 3th and 4th lobe (AI), the number of single teeth on the leaf apex (NT2), the angle of leaf apex (AT) and the angle of leaf base (AB).

For *S. cambrensis,* the PCA showed a geographical pattern with the populations from Llanthony Valley (Capel-y-ffin, Darren, Darren Lwyd), separated from the other populations along the second ordination axis (Fig. 2). The most strongly correlated characters with the second component axis were lamina length (LL), widest point from leaf base (WP), depth of incision between 3nd and 4rd lateral vein from laminar base (I), petiole length (P) and lamina width (LW).

For *S. stenophylla*, the PCA indicated slight separation of the Tarren yr Esgob population along the first component axis (Fig. 2) and also along the third axis (Fig. 3). The most strongly correlated characters with the third component axis were number of teeth at 4th lobe (NT1), number of lateral lamina veins (NV), width of 4th lobe (L), number of single teeth on the leaf apex (NT2) and angle of leaf apex (AT).

The LDA also confirmed the morphological separation of the species. No overlap of canonical scores of the species was detected (Fig. 4). A forward selection procedure identified seven characters (LL:LW, NT1, AI, AB, WP, AT, LW) with significant conditional effects (i.e. the effect of the variable in addition to other variables already included in the model) and these and five additional characters (NT2, AT2, AV, L, AT) with significant marginal effects (i.e. the effect of the variable when alone in the model). The cross-validated discriminant analysis using these seven characters with significant conditional effect resulted in correct classification in all cases.

Within *S. cambrensis,* the LDA analysis showed morphological separation of the Llanthony Valley populations (Fig. 5)**.** A forward selection procedure identified three characters (WP – widest point from leaf base, AT – angle of leaf apex, NT2 – number of single teeth on the leaf apex) with significant conditional effects and nine characters (WP, LL, I, AT, LW, NT1, AB, LL:LW, AI) with significant marginal effects. The cross-validated discriminant analysis using the three characters with significant conditional effect resulted in correct classification in 34 of 36 cases – only two individuals from Llanthony valley were misclassified to the second group.

Within *S. stenophylla*, the LDA analysis confirmed morphological separation of the three sampled populations (Fig. 6). A forward selection procedure identified characters angle of leaf apex (AT) and lamina width (LW) with significant conditional effects and AT, LW, LL:LW, L, AI, AL, NV characters with significant marginal effects. The cross-validated discriminant analysis using the two characters with significant conditional effect resulted in correct classification in five of six cases in the Tarren yr Esgob population (one individual was misclassified to the Darren population). All members of the Govilon population were classified incorrectly to the Darren population and two trees from the Darren population were determined incorrectly to the Govilon population and other two to the Tarren yr Esgob population.

Scans of the leaves are shown in Fig. 7 and elliptic Fourier approximations of the leaves of both species summarised in Fig. 8. These show the narrower leaves with the widest point further above the middle of the leaf in *S. stenophylla* compared to *S. cambrensis*.

Table 3. Univariate statistics (minimum, 5 and 95% percentiles, maximum) of quantitative characters of *Sorbus cambrensis* and *S. stenophylla*.

Taxon/population	*Sorbus cambrensis*/all sampled population	*Sorbus stenophylla* s.str./ Tarren yr Esgob	*Sorbus stenophylla* s.l. / Govilon and Darren
Petiole length (cm)	(0.9–)1.1–1.7(–1.8)	(0.8–)0.9–1.7(–1.8)	(0.9–)1–1.6(–1.8)
Lamina length (cm)	(7.7–)8.2–11.3(–12.2)	(7.6–)7.9–10.5(–10.8)	(7.9–)8.5–10.8(–10.9)
Lamina width (cm)	(5.6–)6.1–7.9(–8.8)	(4.9–)4.9–6.4(–6.5)	(5.3–)5.6–7.2(–7.6)
Width of 4th lobe (cm)	(0.7–)0.8–1.4(–1.7)	(0.5–)0.7–1.2(–1.4)	(0.7–)0.8–1.3(–1.4)
Lamina length/width ratio	(1.2–)1.3–1.5(–1.6)	(1.5–)1.5–1.8(–1.9)	(1.3–)1.4–1.7(–1.8)
Widest point from base as percentage of way along leaf length (%)	(48–)53.1–65.9(–69.5)	(53.7–)55.5–67(–67.5)	(48.1–)52.4–62.9(–69.2)
Depth of lobbing between 3th and 4th lobes as percentage of way to midrib (%)	(3.8–)5.6–14.6(–17.4)	(6.3–)7.3–15.8(–17.2)	(4.7–)6.2–15.6(–18.3)
Apex angle (°)	(116.3–)126.5–157.1(–166.7)	(110–)116.3–141.8(–147.7)	(104.9–)107.2–138(–143.1)
Vein angle (°)	(25.9–)28.5–41.9(–46.5)	(25.6–)26.3–34.8(–35.4)	(23.4–)26.9–36(–39.5)
Base angle (°)	(68.4–)76–101.3(–119.4)	(60–)62.8–79.6(–83.4)	(59.4–)62.9–86.8(–95)
Angle between 3th and 4th lobes (°)	(41.8–)48.6–93.6(–103.6)	(22.8–)28.4–65.4(–71.1)	(27.6–)33.3–74.9(–78.9)
Angle of terminal tooth of 3rth lobe (°)	(58–)68.9–105.4(–118.8)	(36.9–)45.2–75.8(–84.3)	(44.8–)50.1–91.1(–100.6)
Number of veins	(6–)8–10(–10)	(7–)7–9(–10)	(7–)8–10(–10)
Number of teeth at 4th lobe	(2–)3–6(–7)	(2–)2.5–7(–8)	(3–)4–8(–9)
Number of singular teeth on the top of the leaves (left side only)	(0–)1–4(–5)	(0–)0–2(–2)	(0–)0–2(–3)

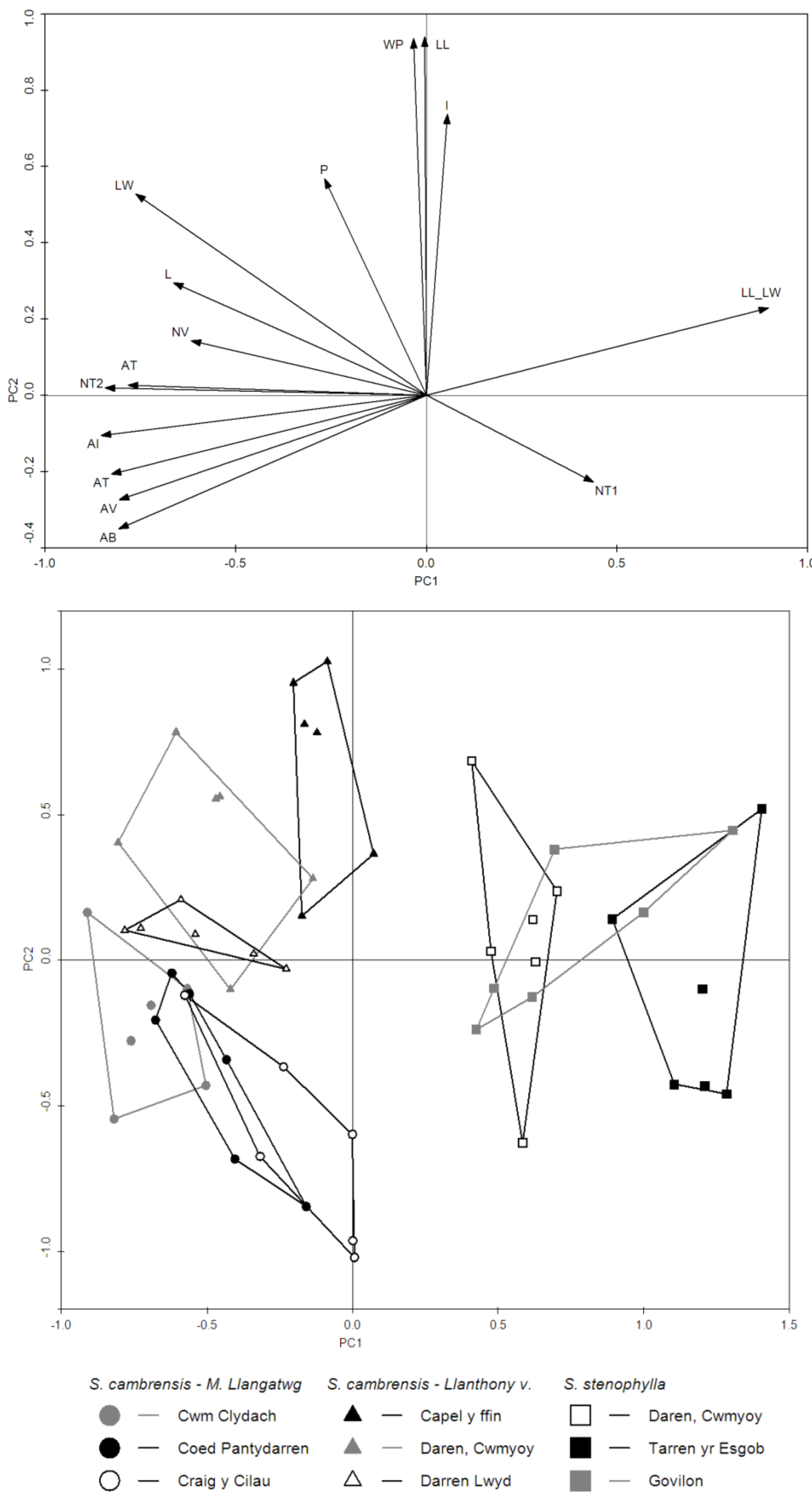

Figure 2. PCA based on 15 morphological characters measured on leaf laminas of six populations of *Sorbus cambrensis* and three populations of *S. stenophylla*. Upper plot: Character loadings. Lower plot: Taxa. The first and second ordination axes explain 43.4% and 22.4% of the overall variation, respectively. For abbreviation of characters, see Methods.

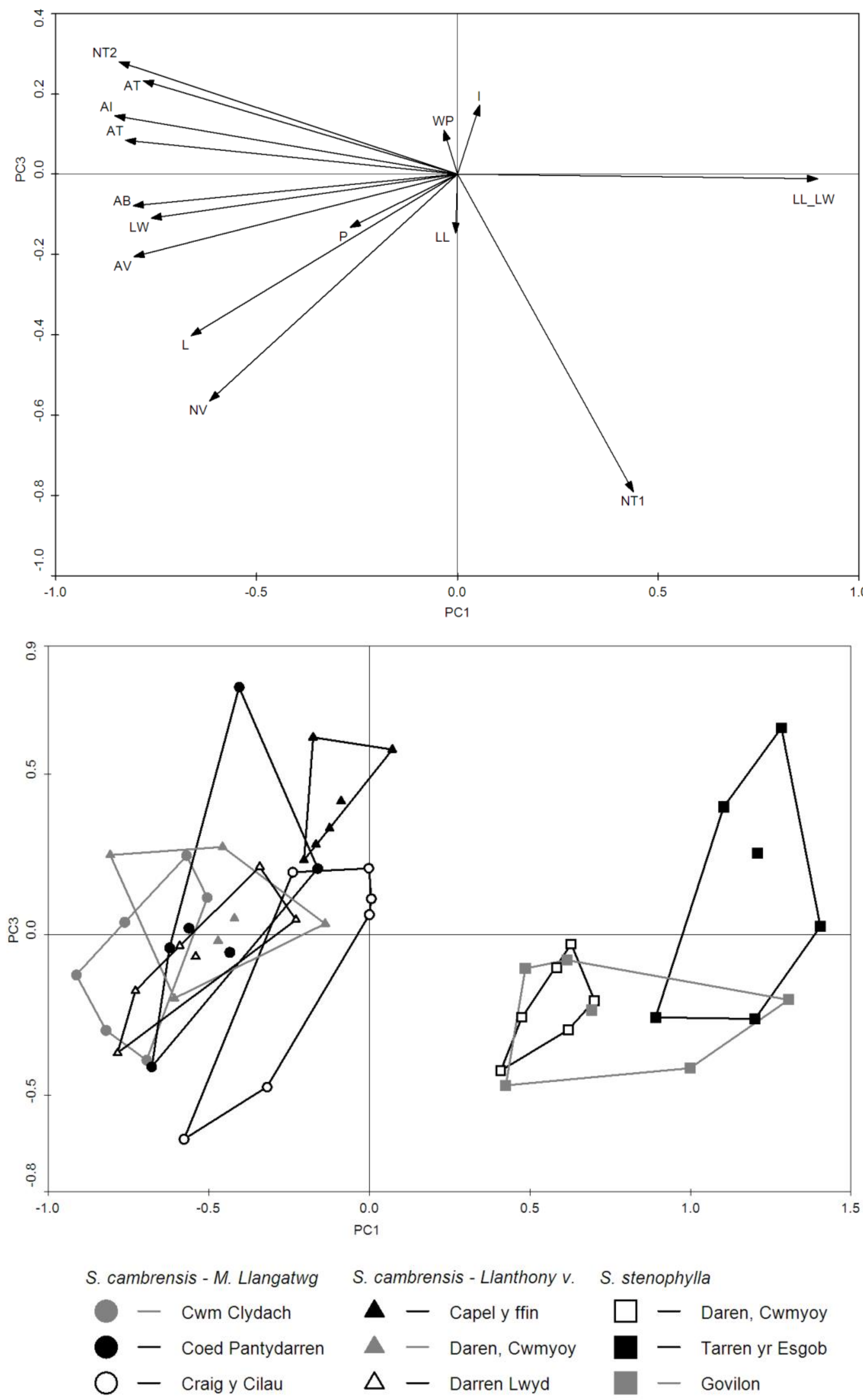

Figure 3. PCA based on 15 morphological characters measured on leaf laminas of six populations of *Sorbus cambrensis* (left) and three populations of *S. stenophylla* (right). Upper plot: Character loadings. Lower plot: Taxa. The first and third ordination axes are displayed and explain 43.4% and 9.4 % of the overall variation, respectively. For abbreviation of characters, see Methods.

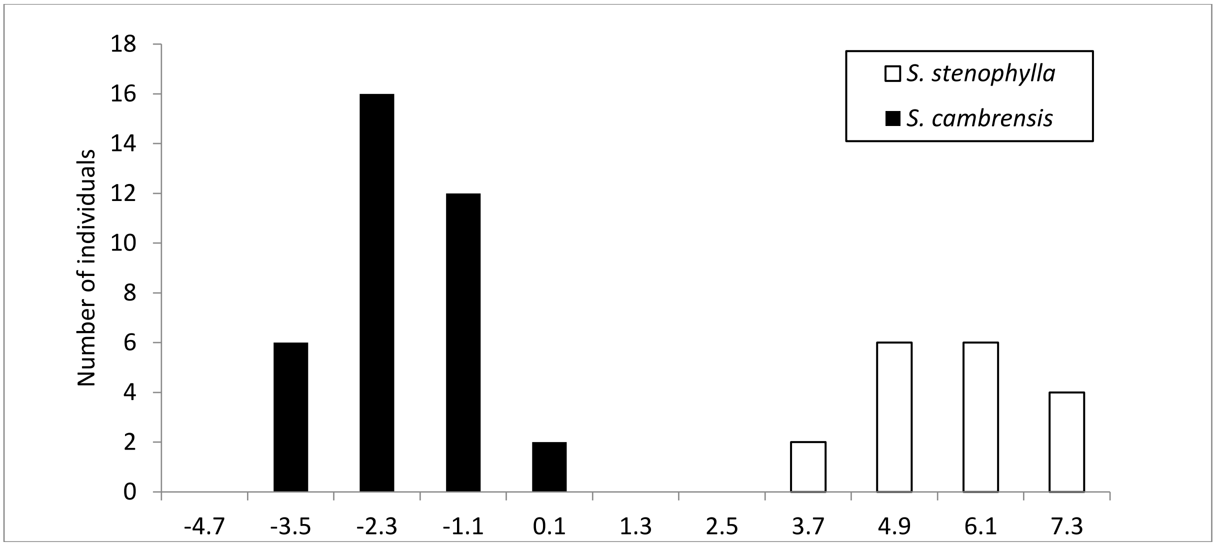

Figure 4. Histogram of canonical scores of linear canonical discriminant analysis based on seven (LL:LW, NT1, AI, AB, WP, AT, LW) morphological characters measured on leaf laminas of six populations of *Sorbus cambrensis* and three populations of *S. stenophylla.* The characters were selected in forward selection procedure, and only those that were significantly different and could be used to distinguish the two taxa were used. The first canonical axis explains 92.9% of the variation. For abbreviation of characters, see Methods.

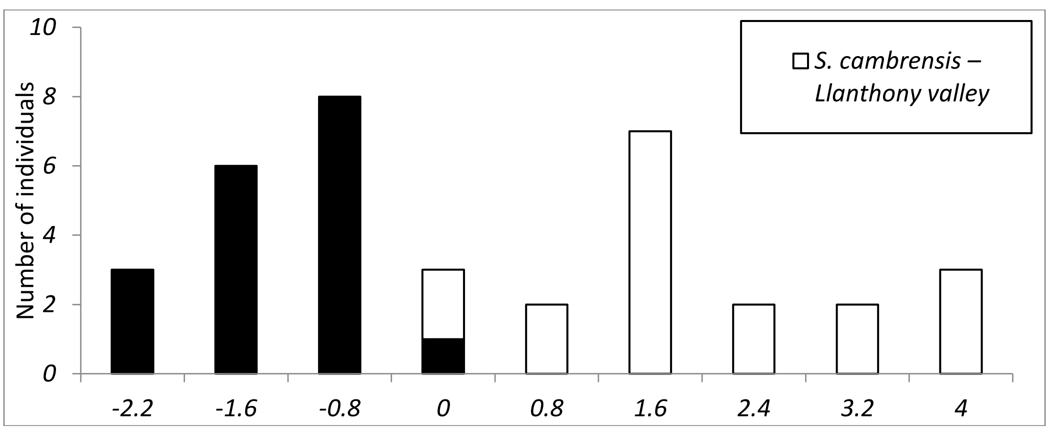

Figure 5. Histogram of canonical scores of linear canonical discriminant analysis based on three morphological characters (WP, AT, NT2) measured on leaf laminas of six populations of Sorbus cambrensis – three from Llanthony valley and three from Mynydd Llangatwg. The characters were selected in forward selection procedure, and only those that were significantly different and could be used to distinguish the two taxa were used. The first canonical axis explains 79.1% of the variation. For abbreviation of characters, see Methods.

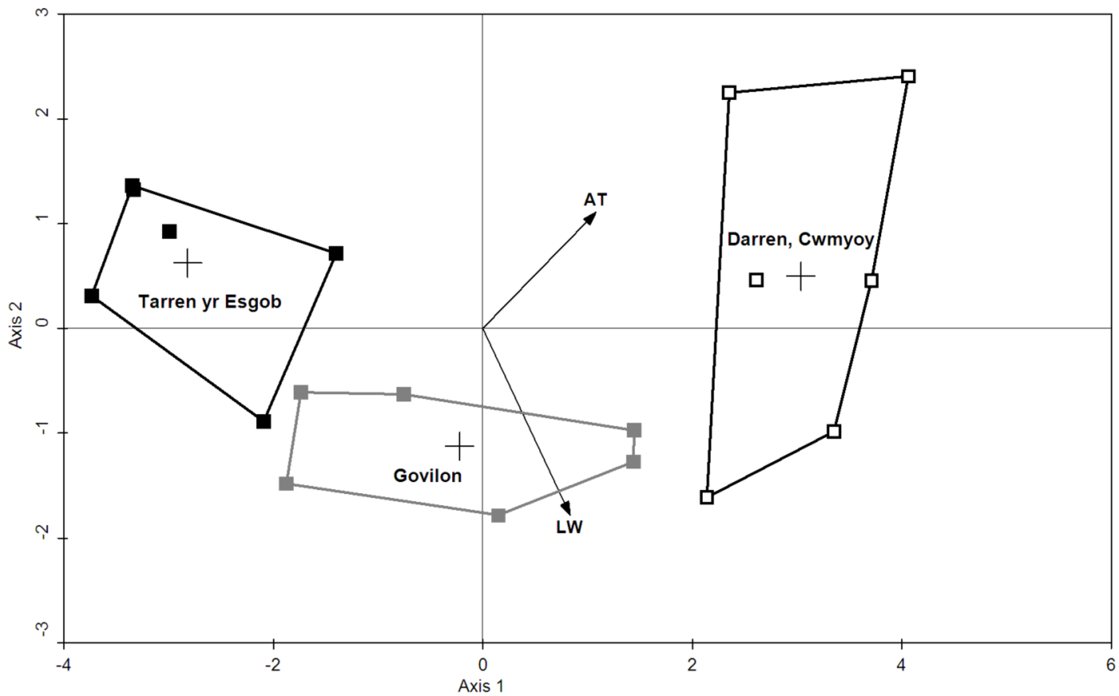

Figure 6. Linear discriminant analysis based on 2 morphological characters of leaves (AT – angle of leaf apex, LW – leaf width) of the three known population of *Sorbus stenophylla*. The characters were selected in a forward selection procedure, and only characters with significant discriminating power for separating the three population were used. The first and second canonical axes are displayed, and explain 42.6% and 19.4% of the variation, respectively.

Discussion

It is now established that both *S. stenophylla* and *S. cambrensis* occur in the Llanthony Valley, and that *S. cambrensis* occurs more widely than previously appreciated. Herbarium material and records from the Llanthony Valley and Black Mountains will need to be revised in light of these findings.

Applying the IUCN (2001) threat criteria to the population data show both *S. cambrensis* and *S. stenophylla* qualify as 'Endangered' (Rivers *et al.,* 2019).

The morphological analysis shows that *S. cambrensis* varies significantly in leaf morphology geographically. The Llanthony Valley populations differed from the Mynydd Llangatwg populations (including the type locality at Cwm Clydach), and within the latter group the population from Craig y Cilau seems to be very variable. Similarly, *S. stenophylla* at the type locality at Tarren-yr-Esgob differs from the plants at Govilon and Darren which have leaves more similar to each other.

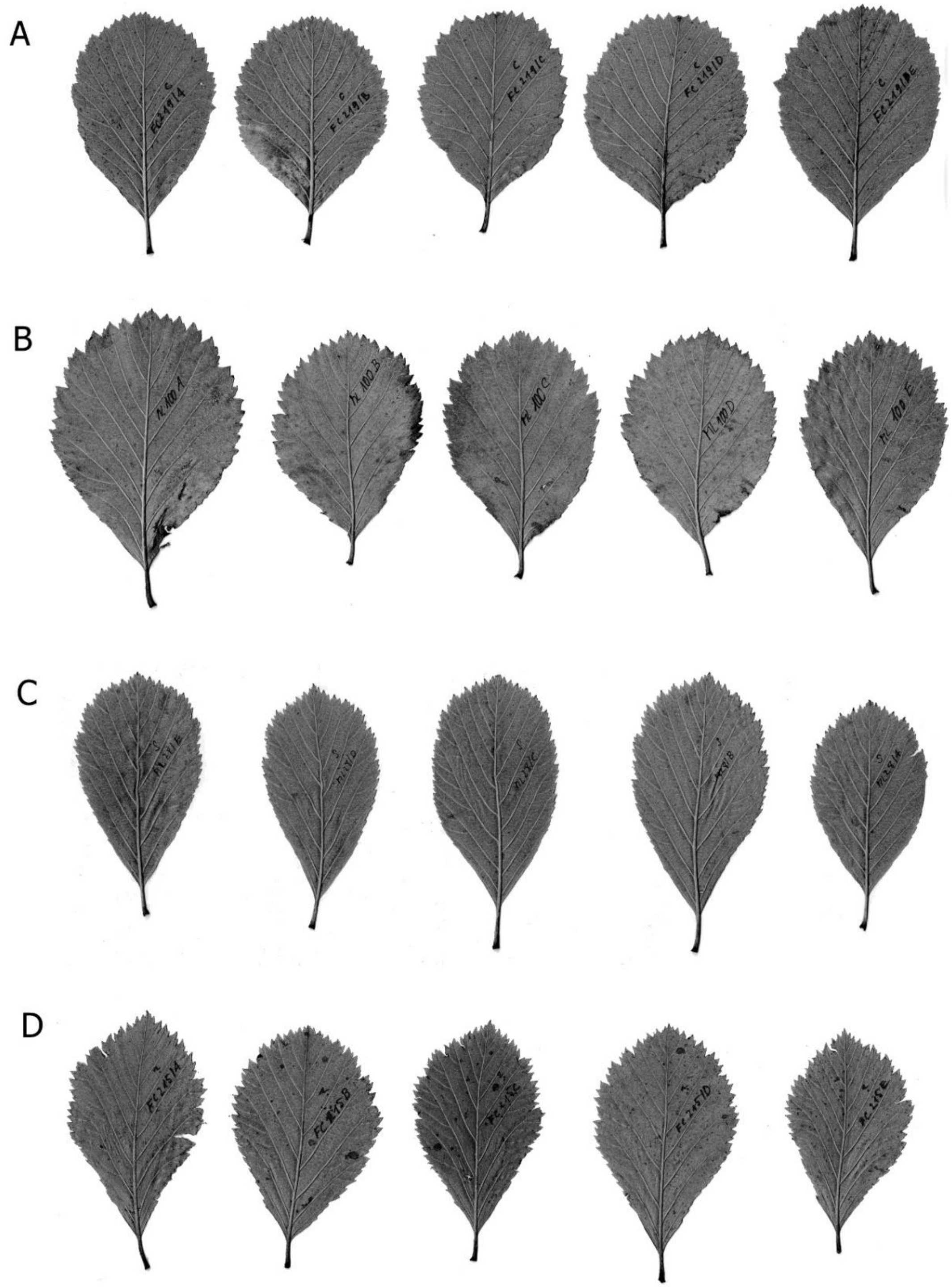

Figure 7. Scans of selected leaves from short lateral shoots of one individual. *Sorbus cambrensis* from A, Cwm Clydach (type locality) and B, Llanthony Valley (Capel-y-ffin). *Sorbus stenophylla* C, Tarren yr Esgob (type locality) and D, Govilon.

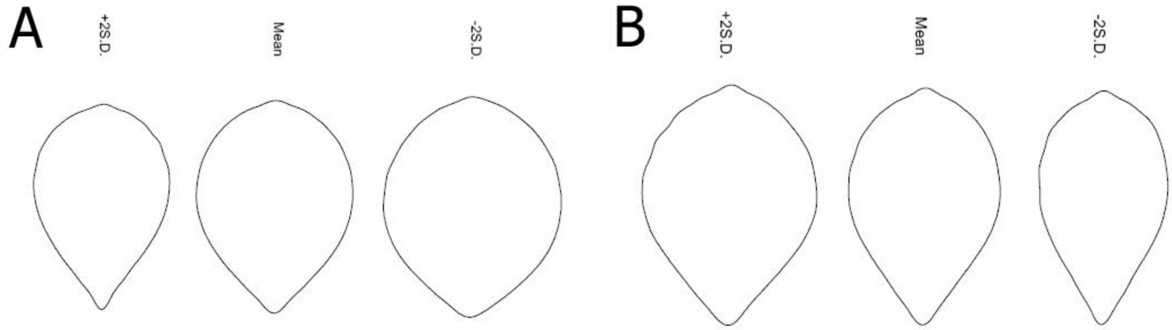

Figure 8. Mean and ±2 standard deviations elliptic Fourier approximations of the leaves of (A) *S. cambrensis* and (B) *S. stenophylla*

The origin of this variation needs further study. The variation could be partly of environmental origin as the conditions at the different localities differ in aspect, altitude and soil type, or could be due to reproductive modes or different origins. *S. cambrensis* and *S. stenophylla* are unusual in being pentaploid (Pellicer *et al.*, 2012) so would be expected to be obligate apomicts (Rich *et al.,* 2010), but studies of the reproductive modes of *S. cambrensis* and *S. stenophylla* using flow cytometry of embryos, endosperm and pollen showed that whilst *S. stenophylla* was fully apomictic, *S. cambrensis* had a prevailing (77%) sexual development of seeds probably fertilized by their own pollen (Lepší *et al.*, 2019). However, as the *S. cambrensis* populations were generally morphologically uniform (except for those at Craig y Cilau), it may be that only seeds/seedlings produced apomictically are viable.

Different origins may also account for some of the variation. As diploids are (currently) absent from the pentaploid distribution ranges, their pentaploid cytology level suggest that *S. cambrensis* and *S. stenophylla* could have originated as hybrids between triploid *S. porrigentiformis* E. F. Warb. *sensu lato* (unreduced female 'gamete' 3n) and tetraploid *S. rupicola* (Syme) Hedl. (reduced pollen 2n). *Sorbus cambrensis* occurs with both these taxa at Craig y Cilau and may have originated there, once or multiple times. *Sorbus cambrensis* may in turn have given rise to *S. stenophylla* which does not overlap with the (current) distributions of the putative parents at all. Furthermore, the obligate apomixis in *S. stenophylla* coupled with field observations that the Tarren yr Esgob population differs from the Darren and Govilon populations more than our leaf morphology analysis above indicates, makes it possible that these populations are also of different origin. Additional research using molecular techniques and flower and fruit morphology should allow these possibilities to be separated, but in the meantime, we maintain the existing taxonomy.

The incorrect tetraploid ploidy level cited for *S. cambrensis* by Rich *et al.,* (2010) was based on a chromosome count of 2n=*c.*68 for a member of *S. porrigentiformis* group from 'Darren Disgwylfa' (i.e. Coed Pantydarren) (Proctor & Groenhof, 1992; Bailey *et al.*, 2008) where only one taxon is now known which is pentaploid *S. cambrensis* (n=6; Pellicer *et al.,* 2012). Similarly, Lemche's (1999) tetraploid 'E2' from Cambridge University Botanic Garden cited by Rich *et al.,* (2010) as *S. cambrensis* is a different, un-named taxon of uncertain origin; Lemche's (1999, Table 8) grid reference

SO220138 also refers to Coed Pantydarren but the locality was cited as the Black Mountains; the Botanic Gardens no longer hold details of this plant which is not now in cultivation (pers. comm. M. Millan 2022). E2 was originally collected by P. D. Sell who regarded it as a "special small-leafed *S. porrigentiformis* type to be described as a new species" (Lemche, 1999, page 68) and differs from other members of subgenus *Aria* by having some contribution from *S. torminalis* but did not match any other subgenus *Tormaria* taxa (Lemche, 1999); being tetraploid it presumably does not match our triploid subgenus *Tormaria* plant from Darren, Cwmyoy (Rich *et al.,* 2014).

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