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Peroxidase isoenzyme and morphological variation in *Sorbus* L. in South Wales and adjacent areas, with particular reference to *S. porrigentiformis* E. F. Warb.

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ABSTRACT

The delimitation of microspecies of *Sorbus* L. (Rosaceae) occurring in South Wales, the Wye Valley, the Bristol area and Mendip is considered in relation to their peroxidase phenotypes and leaf, fruit and growth-habit characters. On isoenzyme evidence, *S. minima* (A. Ley) Hedl., *S. leyana* Wilmott, *S. anglica* Hedl. and *S. bristoliensis* Wilmott all appear essentially uniform and well delimited. *S.* × *vagensis* Wilmott is variable in peroxidase phenotype, as expected of a sexual hybrid. *S. leptophylla* E. F. Warb. appears genetically uniform, but plastic in habit and leaf size. Its established distribution is limited to two localities in Brecs. (v.c. 42); peroxidase evidence and fruit characters confirm a probable relationship to plants on Craig Breidden, Monts. (v.c. 47). *S. eminens* E. F. Warb. from near Symonds Yat is genetically different from plants in the Bristol – Mendip area, which show similarities in peroxidase, leaf, fruit and growth-habit characters to trees on the Menai Straits and to *S. hibernica* E. F. Warb. Plants which have been named *S. porrigentiformis* E. F. Warb. in South Wales include: (a) a widespread plant, of uniform peroxidase phenotype, with obovate leaves and broad crimson fruits, typically forming a twiggy shrub with rather slender shoots (the holotype appears identical with this); and (b) a much more local plant in the Mynydd Llangattock – Cwm Clydach area and the Black Mountains, of different peroxidase phenotype, commonly growing into a small tree, with more oblong biserrate leaves and larger subglobose scarlet fruits. Plants from near Symonds Yat growing with and somewhat resembling *S. porrigentiformis*, differ from both (a) and (b) in peroxidase phenotype. Like *S. porrigentiformis*, they appear more closely related to *S. graeca* (Spach) Kotschy than to *S. aria* (L.) Crantz, sensu stricto; they need further study.

INTRODUCTION

The British species of *Sorbus* L. (Rosaceae) comprise three sexually reproducing diploids, *S. aucuparia* L., *S. aria* (L.) Crantz and *S. torminalis* (L.) Crantz, and a number of polyploids all of which are probably normally apomictic. These form populations of essentially identical individuals which can be recognized as distinct microspecies (Warburg 1952, 1962; Perring & Sell 1968). The microspecies distinguished in the British Isles fall into three groups. The largest number (making up the *S. aria* aggregate) appear to be derivatives of diploid *S. aria* sensu lato. A group including *S. anglica* Hedl. show characters intermediate between *S. aria* sensu lato and *S. aucuparia*; the *S. latifolia* group are similarly intermediate between *S. aria* sensu lato and *S. torminalis*.

All but four of the described microspecies of *Sorbus* in the British Isles occur in the area around the Bristol Channel. The sites at which they grow fall into three broad groups. In an eastern group of sites, on the Carboniferous Limestone of Mendip, the Avon Gorge and the Wye Valley, the apomicts occur in contact with sexual *S. aria* as well as *S. aucuparia* and *S. torminalis*. The other two groups, on the Carboniferous Limestone crags of Breconshire and West Glamorgan and on the Old Red Sandstone of the North Devon and West Somerset coast, are beyond the western limit of *S. aria* and the Whitebeam populations appear to be wholly apomictic.

Sorbus in the Bristol Channel area thus presents a picture of some complexity, and potentially of great interest as a model for studying the evolution and ecology of an apomictic group. Proctor *et al.* (1989) investigated populations in Devon and West Somerset, and showed the usefulness of peroxidase isoenzyme phenotypes in helping to delimit and characterize apomictic *Sorbus* populations. Isoenzymes provide additional characters and make possible an interplay of hypothesis and test between biochemical and morphological evidence; they also extend the possibilities for assessing genetic relationships between populations.

Warburg (1952, 1957) indicated the occurrence of some variation within *S. anglica*, *S. eminens* E. F. Warb. and *S. porrigentiformis* E. F. Warb. The experience of a number of field botanists has suggested that there are real difficulties in the characterization and identification of several of the species, especially *S. porrigentiformis* in South Wales. Warburg (1952) gave chromosome numbers of 2n = 51 and 2n = 68 in that species. In this paper we present the results of a survey of peroxidase phenotypes in apomictic *Sorbus* populations in South Wales and neighbouring areas, and consider the results in relation to some morphological characters of the plants, and their geographical distributions.

MATERIALS AND METHODS

PEROXIDASE ISOENZYMES

Shoot samples were collected in the field in the summers of 1989 and 1990, and brought back fresh to the laboratory. The extracts used for electrophoresis were of 'bark' tissue scraped from (usually) second-year shoots. They were made as soon as possible after collection, but we found that even in summer shoots remained in good condition for a week or more if kept in polythene bags in a refrigerator. The extracts were run on vertical polyacrylamide slab gels. Details of the methods used are given by Proctor *et al.* (1989), and the conventions used to describe peroxidase phenotypes here are the same as in that paper. The bands obtained on the gels can conveniently (but arbitrarily) be divided into six groups (Fig. 1). Two slow-running groups (A and B) and a fast-running band (F) tend to be rather diffuse and present in most or all samples, so are of little taxonomic interest. Bands in groups C and E are well defined, and occur in varying combinations in all the British apomictic *Sorbus* species. One or two bands of group D, characteristic of *S. aucuparia*, occur in the apomicts of the *S. anglica* group.

LEAF, FLOWER AND FRUIT CHARACTERS

We collected herbarium material from most of the populations we examined; the specimens have been retained by M.C.F.P. In addition, we collected and pressed a number of samples of representative individual leaves from short shoots; these were photocopied as a convenient means for record and comparison. The colour of both leaf surfaces was recorded from some of the material while still fresh by matching with the R.H.S. Colour Chart (Royal Horticultural Society 1966). Fresh pollen samples from flowers collected in June 1989 were examined microscopically after staining in aceto-carmine, and samples from the same inflorescences were tested for germination in 15% sucrose solution. Fruit was collected in September and early October. Length and breadth of samples of well-formed fruits were measured to the nearest 0·2 mm using a sliding caliper-rule. To provide a reproducible and quantitative basis for recording fruit colour, fresh fruits were matched with a limited sub-set of the shades in the R.H.S. Colour Chart, chosen so that their coordinates in the system of the *Commission Internationale d'Eclairage* (C.I.E.) formed a reasonably evenly graded series. Individual fruits tend to run through the whole or a part of this series as they ripen; broad differences between species are easily established, but for rigorous comparisons fruits need to be at the same stage of ripeness. The C.I.E. chromaticity and reflectance coordinates for the shades used are given in Appendix 1.

RESULTS

The peroxidase phenotypes found in our material are summarized diagrammatically in Fig. and the fruit measurements in Table 1.

S. ANGLICA AND ITS ALLIES

Samples of *S. anglica* from the Mynydd Llangattock area, the Wye Valley, the Avon Gorge,

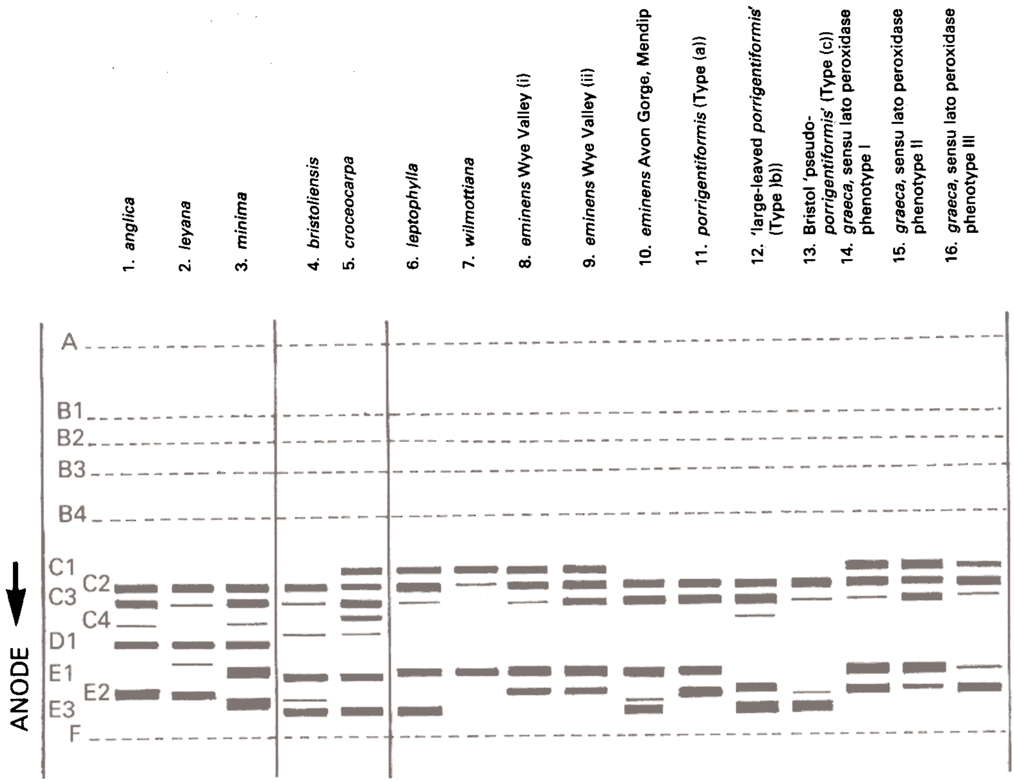


FIGURE 1. Schematic diagram of peroxidase phenotypes of apomictic *Sorbus* populations from South Wales and adjoining areas. Conventions follow Proctor *et al.* (1989).

Cheddar, Breidden and Llangollen all show the same peroxidase phenotype as that found in a plant of Avon Gorge origin by Proctor *et al.* (1989). The trees varied slightly in leaf shape but in general had somewhat more angular and deeply incised lobes than plants from Devon (Fig. 2). There appears also to be a consistent difference in fruit shape between trees on Breidden and those farther south (Table 1).

The geographically very restricted *S. minima* (A. Ley) Hedl. (five trees) and *S. leyana* Wilmott (three trees) show consistent and distinctive peroxidase phenotypes. In *S. minima* Proctor *et al.* (1989) indicated a pair of bands in positions D2 and E1; the latter generally stains more strongly and the two are often not clearly resolved. Pollen of both species showed virtually no germination in 15% sucrose solution, and a large proportion of misshapen and empty grains, suggesting that both are probably triploid (Liljefors 1953).

THE *S. LATIFOLIA* GROUP

Four trees of *S. bristoliensis* Wilmott from the Leigh Woods side of the Avon Gorge were consistent in their peroxidase phenotype, erroneously shown by Proctor *et al.* (1989) as including band C4; this is absent in *S. bristoliensis*, although the weak band C5 is present. *S. croceocarpa* (Sell 1989), of which there are planted and naturalized trees around Bristol, has a peroxidase phenotype differing from that of *S. devoniensis* E. F. Warb. most conspicuously in the very much stronger band C3; the same phenotype is found consistently in material from the type area in Anglesey and at Nantporth on the Bangor side of the Menai Straits.

Four trees of *S.* × *vagensis* Wilmott all gave different peroxidase phenotypes, a result consistent with the supposition that this is a sporadically occurring sexual hybrid.

TABLE 1. FRUIT DIMENSIONS AND COLOURS FROM *SORBUS* POPULATIONS, SEPTEMBER–OCTOBER 1989–90

Fruit dimensions are given for individual trees; n is the number of fruits measured. Length/breadth ratios were calculated individually for each fruit. Fruit colour assessments are based on all the material available from a particular locality at the time of scoring.

Species and locality	n	Length mean (s.d. (mm)	Breadth mean (s.d. (mm)	Length/breadth mean (s.d.)	Fruit colour (R.H.S. Colour Chart)
S. aucuparia					
Countisbury, N. Devon (v.c. 4)					44A(–45A)
Lynmouth, N. Devon (v.c. 4)					33A
S. anglica					
N. Whilborough Common, S. Devon (v.c. 3) (i)	10	10·2 (0·51)	11·0 (0·46)	0·93 (0·036)	44A–45A
(ii)	10	9·9 (0·86)	10·6 (0·50)	0·93 (0·051)	,,
Woody Bay, N. Devon (v.c. 4)	10	11·0 (0·43)	12·4 (0·62)	0·89 (0·045)	(44A–)45A
Cheddar, N. Somerset (v.c. 6)					
(i)	8	10·8 (0·64)	11·8 (1·07)	0·91 (0·039)	45A(–46A)
(ii)	10	10·9 (0·56)	11·9 (0·29)	0·92 (0·038)	,,
Lover's Leap, Mons. (v.c. 35)	10	10·7 (0·63)	11·6 (0·94)	0·92 (0·024)	45A
Cwm Clydach, Glam. (v.c. 41)	10	10·9 (0·68)	11·6 (0·63)	0·95 (0·080)	44A(–45A)
Breidden, Monts. (v.c. 47)					
(i)	5	10·1 (0·48)	10·1 (0·44)	1·00 (0·037)	45B
(ii)	5	10·6 (0·22)	10·6 (0·61)	1·00 (0·047)	
(iii)	5	11·7 (0·52)	11·3 (0·50)	1·04 (0·059)	
(iv)	5	11·2 (0·88)	11·4 (0·68)	0·98 (0·052)	
S. aria					
Cheddar, N. Somerset (v.c. 6)					
(i)	5	12·4 (0·43)	12·7 (0·56)	0·98 (0·035)	(33A–)44A(–45A)
(ii)	15	14·1 (0·77)	13·6 (0·68)	1·04 (0·048)	
(iii)	10	12·3 (0·39)	13·5 (0·55)	0·91 (0·045)	
(iv)	10	11·4 (1·09)	11·3 (0·97)	1·01 (0·034)	,,
Seven Sisters Rocks, Herefs. (v.c. 36)	10	12·8 (0·79)	11·6 (1·25)	1·09 (0·079)	(28A–)32A(–33A)
S. leptophylla					
Craig-y-Rhiwarth, Brecs. (v.c. 42)					
(i)	15	14·7 (0·56)	13·8 (0·64)	1·07 (0·058)	(44A–)45A
(ii)	6	14·3 (0·73)	13·0 (0·61)	1·10 (0·037)	
(iii)	9	14·4 (0·32)	13·1 (0·52)	1·11 (0·043)	
(iv)	8	13·3 (0·68)	12·5 (0·43)	1·07 (0·053)	,,
Craig-y-Cilau, Brecs. (v.c. 42)	10	14·8 (0·71)	14·3 (0·63)	1·04 (0·057)	44A–45A
S. aff. *leptophylla*					
Breidden, Monts. (v.c. 47)	5	14·3 (0·30)	11·6 (0·75)	1·23 (0·067)	
S. wilmottiana					
Bristol, W. Gloucs. (v.c. 34)	10	10·7 (0·54)	10·4 (0·61)	1·03 (0·035)	
S. eminens					
Bristol, W. Gloucs. (v.c. 34)	10	13·8 (0·77)	15·4 (0·64)	0·89 (0·029)	(44A–)45A
Leigh Woods, N. Somerset (v.c. 6)	15	12·0 (0 92)	13·8 (0·91)	0·87 (0·045)	(33A–)44A–45A(–46A)
Worlebury, N. Somerset (v.c. 6)	10	12·7 (0·81)	14·0 (0·62)	0·91 (0·057)	45A–46A

TABLE 1. *continued*

Species and locality		Length mean (s.d. (mm)	Breadth mean (s.d. (mm)	Length/breadth mean (s.d.)	Fruit colour (R.H.S. Colour Chart)
Cheddar, N. Somerset (v.c. 6)					
(i)	5	10·9 (1·12)	13·2 (1·01)	0·83 (0·056)	(44A–)45A–46A
(ii)	3	14·2 (1·06)	16·5 (0·64)	0·86 (0·031)	
(iii)	10	12·0 (0·32)	14·3 (0·42)	0·85 (0·030)	
(iv)	10	11·2 (0·38)	13·4 (0·61)	0·84 (0·029)	
Seven Sisters Rocks, Herefs. (v.c. 36) (i)	5	10·6 (0·39)	11·5 (0·18)	0·97 (0·034)	45A
(ii)	4	10·2 (0·19)	11·6 (0·52)	0·88 (0·043)	
S. aff. *eminens*					
Bangor, Caerns. (v.c. 49)					
(i)	12	12·0 (0·66)	13·4 (0·46)	0·90 (0·044)	45A(–46A)
(ii)	10	11·2 (0·39)	13·2 (0·79)	0·86 (0·031)	
S. hibernica					
Dromineer, N. Tipperary (v.c. H10)	12	13·8 (0·65)	14·8 (0·58)	0·94 (0·032)	(44A–)45A
Rathdrum, Co. Wicklow (v.c. H20)		12·3 (0·46)	13·2 (0·39)	0·93 (0·028)	
S. porrigentiformis					
('Type (a)')					
Anstey's Cove, S. Devon (v.c. 3)	20	10·6 (1·11)	13·8 (1·22)	0·78 (0·067)	46A
Woody Bay, N. Devon (v.c. 4)	10	9·1 (0·68)	11·8 (0·58)	0·78 (0·045)	45A–46A–53A
Cheddar, N. Somerset (v.c. 6)	9	10·2 (0·55)	13·4 (0·93)	0·77 (0·035)	46A–53A
Heale Ladder, N. Somerset (v.c. 6)	10	9·3 (0·18)	11·0 (0·17)	0·84 (0·041)	(45A–)46A(–53A)
Wick Rocks, N. Somerset (v.c. 6)	10	10·6 (0·42)	12·4 (0·38)	0·86 (0·033)	46A(–53A)
Craig-y-Rhiwarth, Brecs. (v.c. 42) (i)	10	9·6 (0·50)	11·4 (0·40)	0·85 (0·049)	45A–46A
(ii)	10	9·8 (0·49)	12·3 (0·37)	0·80 (0·035)	
Craig-y-Cilau, Brecs. (v.c. 42)	10	9·0 (0·52)	11·7 (0·40)	0·78 (0·034)	45A
Aberedw Rocks, Rads. (v.c. 43)	10	10·8 (0·62)	13·0 (0·86)	0·84 (0·042)	
('Type (b)')					
Daren Disgwylfa, Brecs. (v.c. 42) (i)	10	11·0 (0·61)	12·4 (0·45)	0·90 (0·028)	44A–45A(–46A)
(ii)	10	12·2 (0·67)	13·7 (0·48)	0·90 (0·042)	
(iii)	10	11·2 (1·15)	12·0 (0·82)	0·93 (0·043)	
Blackrock, Glam. (v.c. 41)	7	11·8 (0·24)	12·0 (0·58)	0·99 (0·035)	45A
Craig-y-Cilau, Brecs. (v.c. 42)	5	11·4 (0·59)	13·6 (0·40)	0·84 (0·026)	(33A–)44A(–45A)
Cwm Clydach, Glam. (v.c. 41)					
(i)	6	11·3 (0·70)	12·0 (0·69)	0·94 (0·064)	45A
(ii)	3	11·1 (0·42)	12·7 (0·12)	0·88 (0·025)	
(iii)	10	12·2 (0·64)	12·6 (0·40)	0·97 (0·037)	
Daren Lwyd, Brecs. (v.c. 42)	4	12·4 (0·75)	12·7 (0·75)	0·98 (0·022)	
Taren-yr-Esgob, Mons./Brecs. (v.c. 35/42)		11·6 (0·27)	3·6 (0·33)	0·86 (0·011)	

TABLE 1. *continued*

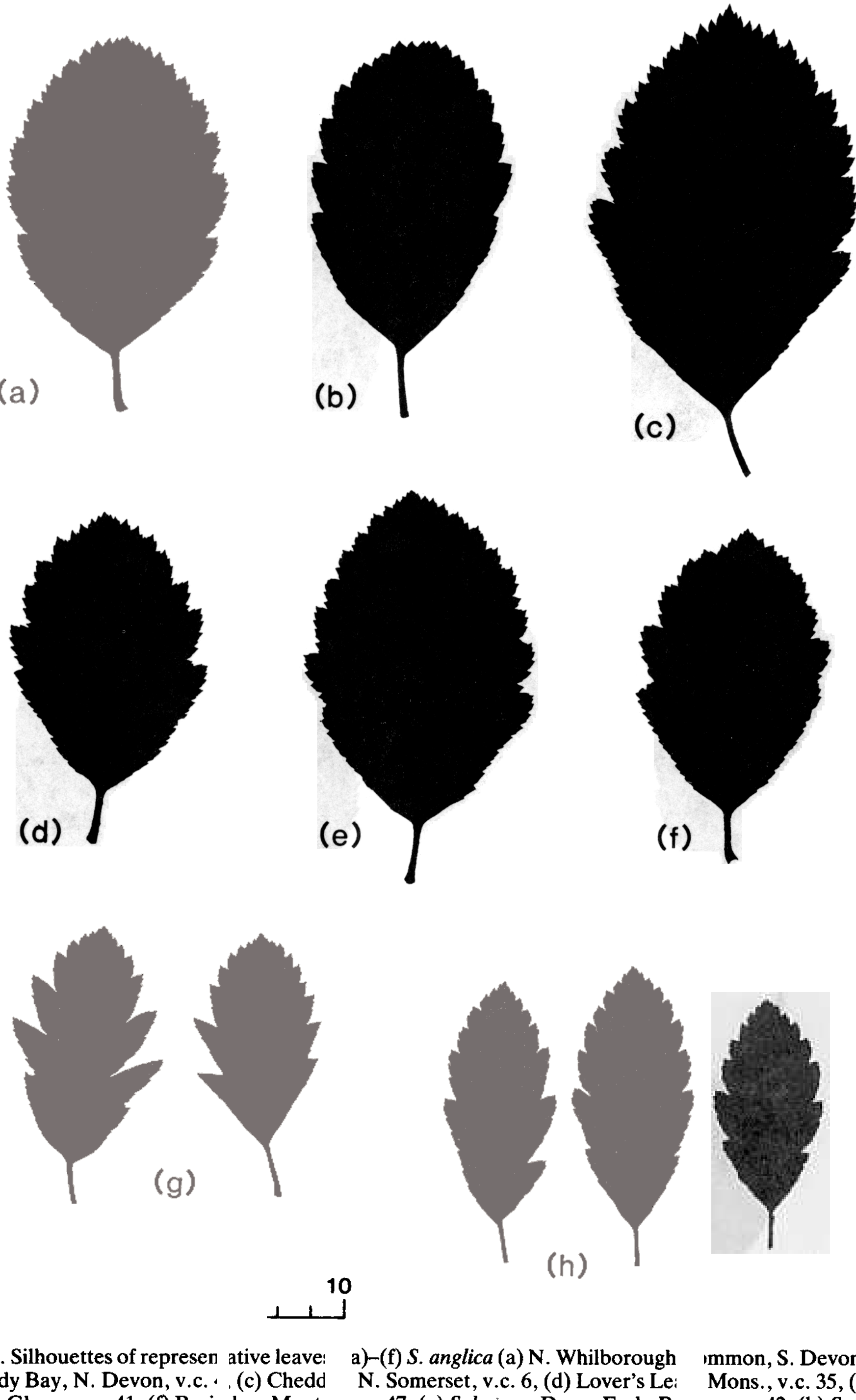
Species and locality	n	Length mean (s.d.) (mm)	Breadth mean (s.d.) (mm)	Length/breadth mean (s.d.)	Fruit colour (R.H.S. Colour Chart)
S. graeca, sensu lato, Seven Sisters Rocks, Herefs. (v.c. 36)					
Peroxidase phenotype I					
(i)	5	10·2 (0·37)	12·6 (0·57)	0·82 (0·039)	45A–46A
(ii)	15	10·7 (0·59)	12·9 (0·61)	0·83 (0·036)	46A
(iii)	6	10·9 (0·43)	13·3 (0·43)	0·82 (0·026)	
(iv)	5	9·6 (0·33)	12·5 (0·64)	0·78 (0·018)	,,
(v)	10	10·1 (0·63)	12·2 (0·45)	0·83 (0·025)	46A–53A
Peroxidase phenotype II	5	11·0 (0·66)	12·2 (0·58)	0·90 (0·038)	(45A–)46A
Peroxidase phenotype III	7	10·8 (0·41)	11·9 (0·67)	0·91 (0·043)	46A
S. rupicola					
Brixham, S. Devon (v.c. 3)					
(i)	6	12·8 (0·58)	14·3 (0·50)	0·90 (0·021)	(33A–)44A(–45A)
(ii)	10	12·1 (0·91)	13·6 (0·87)	0·89 (0·026)	
(iii)	10	11·4 (0·85)	13·5 (0·72)	0·85 (0·029)	
Trentishoe, N. Devon (v.c. 4)	10	13·0 (0·62)	14·9 (0·60)	0·87 (0·041)	45A–46A
Breidden, Monts. (v.c. 47)					
(i)	5	11·2 (0·36)	12·6 (0·56)	0·89 (0·015)	
(ii)	5	10·5 (0·23)	11·7 (0·23)	0·90 (0·023)	
(iii)	5	11·0 (0·70)	12·3 (0·42)	0·89 (0·042)	
Tighnabruaich, Main Argyll (v.c. 98)		12·0 (—)	12·8 (—)	0·94 (—)	

THE *S. ARIA* GROUP

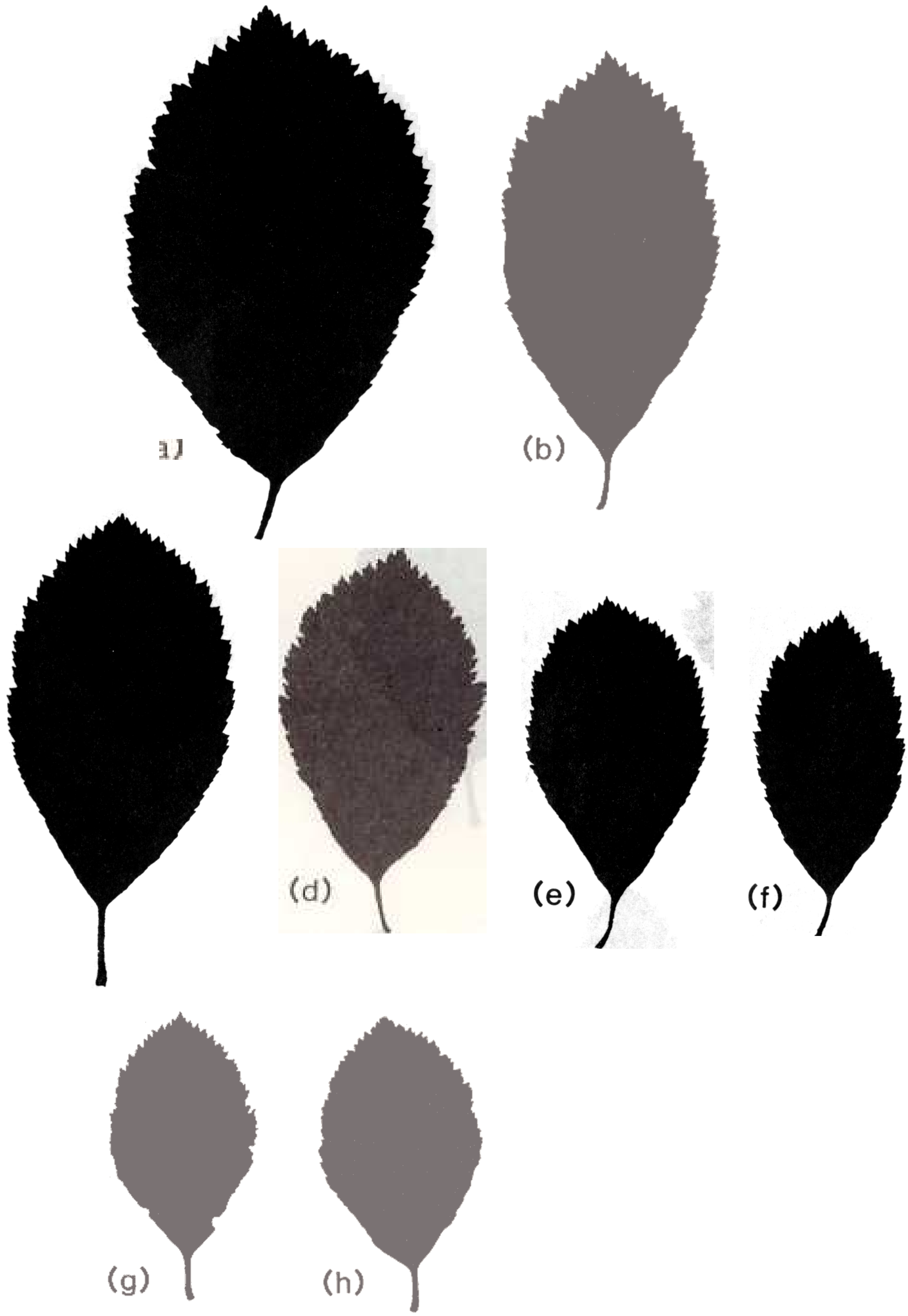
S. leptophylla E. F. Warb. most characteristically forms a sprawling tree with long more or less pendulous branches and large leaves (Fig. 3a–b), rooted into shady vertical limestone cliff faces. Plants of this form grow at both of its two known Breconshire localities, and at both sites have the same constant peroxidase phenotype. It is probably fortuitous that this matches that of 'Taxon D', an unnamed apomict from the North Devon – West Somerset coast, resembling *S. vexans* E. F. Warb. but with broader and darker red fruits (Proctor *et al.* 1989), as the two plants are quite different in habit and leaf and fruit characters. At Craig-y-Rhiwarth *S. leptophylla* is the predominant species (Fig. 3c–f), and the erect individuals in full sun at the top of the cliff appear at first sight very different from those beneath the tree canopy. It is evidently plastic, and small trees can be difficult to distinguish vegetatively from the biserrate-leaved *porrigentiformis*-like plant that accompanies it at Craig-y-Cilau. We have no evidence of its occurrence anywhere in South Wales other than the two localities mentioned. Pollen samples showed a high percentage of well-formed grains and good germination in 15% sucrose solution.

Warburg (1957) indicated that *S. leptophylla* probably occurred also in Montgomeryshire (on Craig Breidden). Some plants on the west crags of Breidden have leaves similar in shape to typical *S. leptophylla* but smaller (Fig. 3g–h). One tree of this type that we sampled appears identical in peroxidase phenotype with Breconshire *S. leptophylla*, and has fruits similar in size, shape, colour and lenticel size and distribution. Specimens collected on the north crags of Breidden by P. J. M. Nethercott in 1990 may also belong to the same form, their somewhat larger leaves reflecting response to a shadier and less drought-stressed habitat.

S. wilmottiana E. F. Warb. (Warburg 1962, 1967) is a rare species of the Avon Gorge at Bristol. We have been able to examine only two trees, which gave a distinctive peroxidase phenotype (C1 C2 E1).



IGURE 2. Silhouettes of represen ative leave a)–(f) *S. anglica* (a) N. Whilborough mmon, S. Devon, v b) Woody Bay, N. Devon, v.c. , (c) Chedd N. Somerset, v.c. 6, (d) Lover's Le Mons., v.c. 35, (e) lydach, Glam., v.c. 41, (f) Brei den, Mont v.c. 47; (g) *S. leyana*, Daren Fach, B ., v.c. 42; (h) *S. min* raig-y-Cilau, Brecs., v.c. 42.


(b)
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(e)
(f)
(g)
(h)

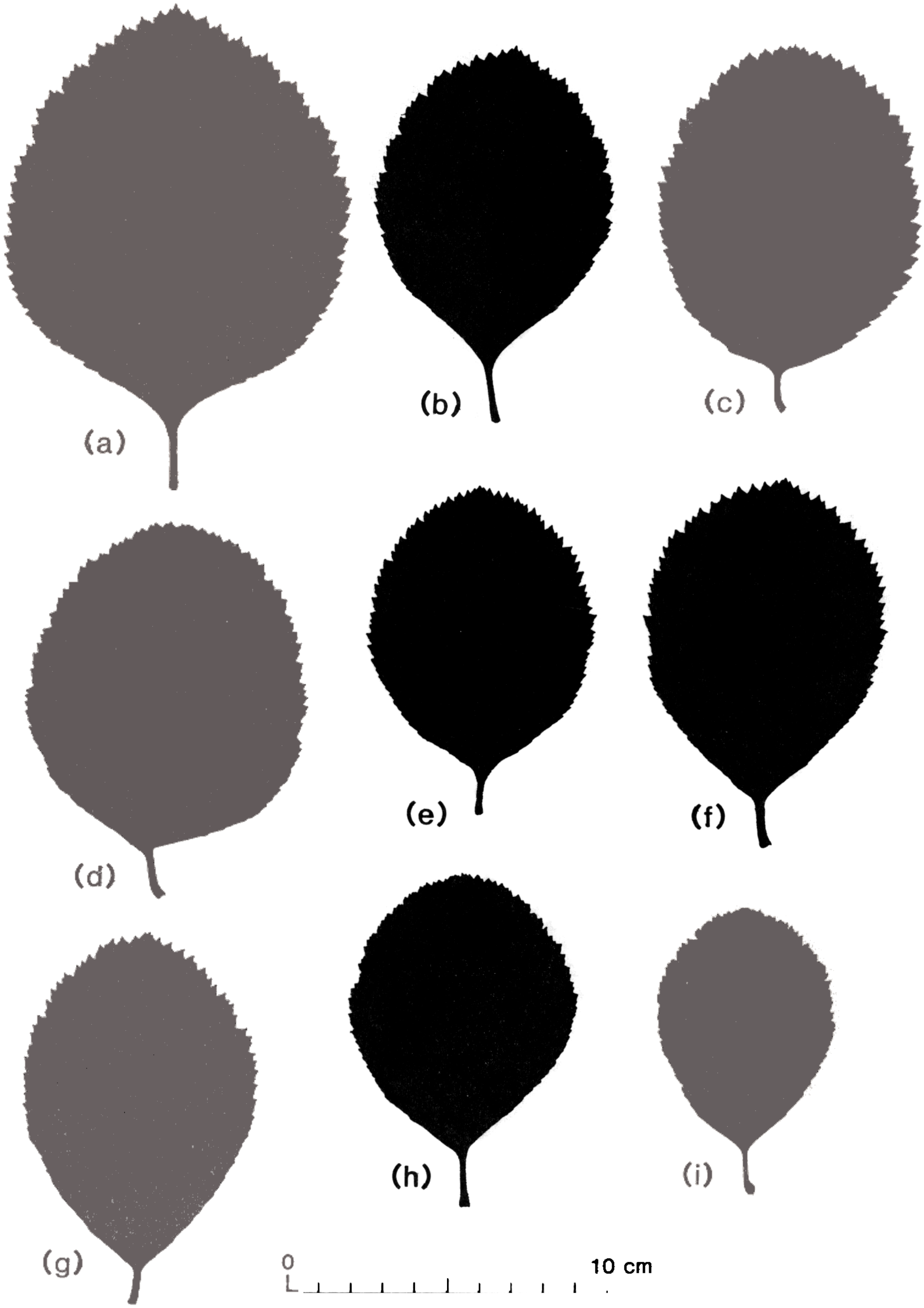

FIGURE 4. Silhouettes of representative leaves of *S. eminens* sensu lato, and related populations. (a) Seven Sisters Rocks, Herefs., v.c. 36 (Wye Valley phenotype (i)), (b) Seven Sisters Rocks (Wye Valley phenotype (ii)), (c) Leigh Woods, N. Somerset, v.c. 6, (d) Bristol, W. Gloucs., v.c. 34, (e) Worlebury, N. Somerset, v.c. 6, (f) Cheddar, N. Somerset, v.c. 6, (g) Nantporth, Bangor, Caerns., v.c. 49, (h) *S. hibernica*, Dromineer, N. Tipperary, v.c. H10, (i) *S. hibernica*, Rathdrum, Co. Wicklow, v.c. H20.

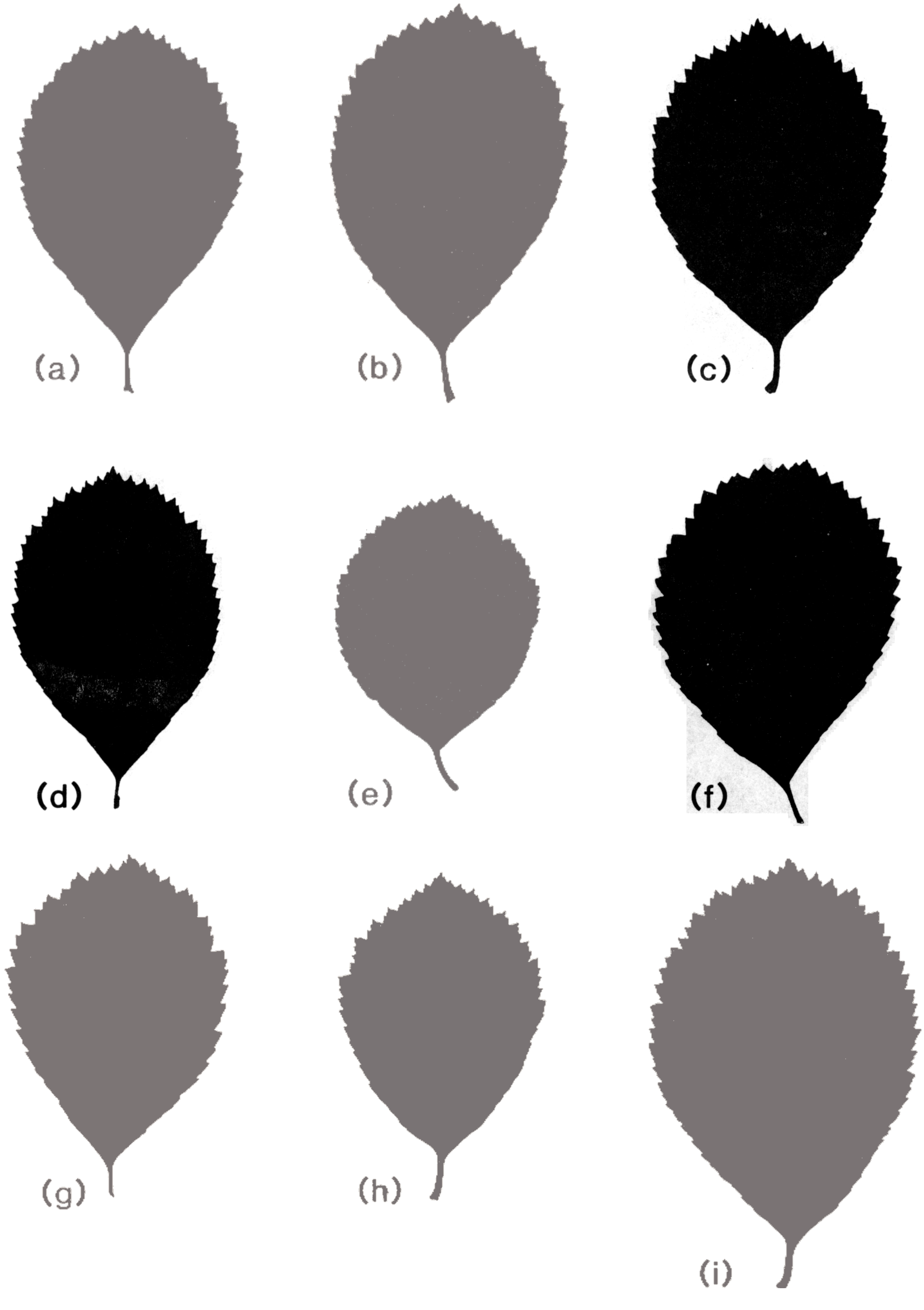

FIGURE 5. Silhouettes o representative leaves of *S. porrigentif mis* and related apomictic populatio *porrigentiformis* (Type)) (a) Babbacombe, S. Devon, v. . 3, (b) Wick Rocks, W. Gloucs., .c. 34 Cheddar, N. Somerset, c. 6, (d) Leigh Woods, N. Somerse v.c. 6, (e) Seven Sisters Rocks, Her (f) Nicholaston, Glam. .c. 41, (g) Craig-y-Rhiwarth, Brec , v.c. 42, (h) Craig-y-Cilau, Brecs., 4 Aberedw, Rads., v.c. 4

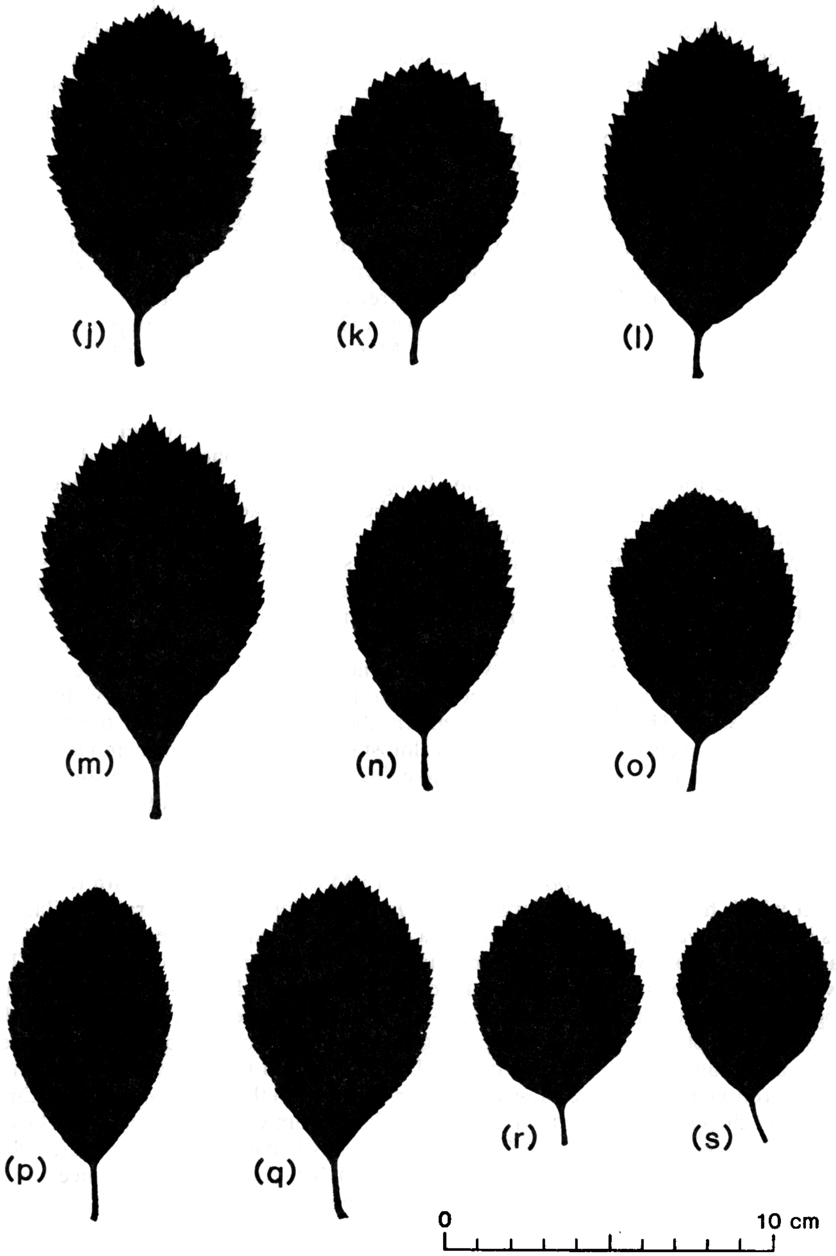

Fig. 5. *continued*
(j)–(o) 'large-leaved *porrigentiformis*' (Type (b)) (j) Cwm Clydach, Glam., v.c. 41, (k) Daren Disgwylfa, Brecs., v.c. 42, (l) Craig-y-Cilau, Brecs., v.c. 42, (m) Taren-yr-Esgob, Mons./Brecs., v.c. 35/42, (n) Daren Lwyd, Brecs., v.c. 42, (o) Cwmyoy, Mons., v.c. 35; (p) Bristol Type (c), Leigh Woods, N. Somerset, v.c. 6; (q)–(s) *S. graeca* sensu lato, Seven Sisters Rocks, Herefs, v.c. 36, (q) peroxidase phenotype I, (r) peroxidase phenotype II, (s) peroxidase phenotype III. Leaves (e), (o), (r) and (s) are from material collected at flowering time in late May; their small size is mainly due to this, rather than inherent difference from other comparable populations.

S. eminens E. F. Warb. was described (Warburg 1952, 1957) as occurring in woods on the Carboniferous Limestone of the Wye Valley and the Avon Gorge. Three trees from shady beech woodland above Seven Sisters Rocks (Fig. 4a), and a small plant with similarly shaped but smaller and firmer leaves in nearby open rocky scrub all showed a constant peroxidase phenotype (C1 C2 (C3) E1 E2); two further trees of similar leaf shape (Fig. 4b) differed in showing a stronger band C3. Warburg (1957) stated that *S. eminens* around Symonds Yat has proportionately longer, more rhomboid and more deeply-toothed leaves than plants from the lower Wye Valley or the Avon Gorge. We have found no trees of *S. eminens* matching the Avon Gorge form in the lower Wye Valley. Herbarium specimens from this area, including Warburg's type in **BM**, appear essentially similar to other Wye Valley material, and agree well with Warburg's description and illustration.

Samples collected from a uniform population in the shady lower fringe of Leigh Woods in the Avon Gorge showed a constant peroxidase phenotype (C2 C3 E1 E3). We found the same peroxidase phenotype in uniform populations of trees in rocky grassland or open scrub near Weston-super-Mare and in Cheddar Gorge. The Avon Gorge and Mendip populations are similar in most leaf, fruit and growth-habit characters; the Mendip plants have rather firmer leaves with a broadly cuneate base and their fruits have larger lenticels. Field observation suggests that the difference in leaf texture may be mainly due to the more exposed habitat of the Mendip trees, but that the difference in shape of the leaf base is, at least in part, genetic. Two other *Sorbus* populations resemble the Avon Gorge and Mendip '*S. eminens*' in peroxidase phenotype and leaf characters. These are a population at Nantporth near Bangor, Gwynedd, which has been named *S. porrigentiformis* but is clearly not that species, and the widespread Irish *S. hibernica* E. F. Warb. Both have fruits similar in size, shape and colour to the Avon Gorge plant (Table 1).

S. porrigentiformis is by far the most widely recorded species in our area. There are at least four clearly different peroxidase phenotypes which correlate with morphological characters (Fig. 5, Table 1), and appear relevant to a satisfactory delimitation of this species.

(a) The most widespread, with peroxidase phenotype C2 C3 E1 E2, occurs throughout the recorded range of the species from Torbay and Gower to Radnorshire and the Bristol-Mendip area. It is typically an open shrub (rarely a small tree) with rather angular and 'twiggy' branching, and relatively slender twigs. The leaves are dark green above (usually 147A on the R.H.S. Colour Chart), obovate, with an entire cuneate base and almost simple outwardly directed teeth (Fig. 5a–i); the fruit is broader than long (length/breadth ratio c. 0·75–0·85), and a deep crimson red when ripe. Samples of pollen from Gower and Craig-y-Rhiwarth showed 72–84% of well-filled grains and about 20% germination in 15% sucrose solution; Dr Q. O. N. Kay has obtained chromosome counts of 2n = (67–)68 in plants from Woody Bay (v.c. 4), Wick Rocks (v.c. 34) and Craig-y-Cilau (v.c. 42) (unpublished). The holotype of *S. porrigentiformis* in **BM** appears identical with this form.

(b) The plant which has been called 'large-leaved *porrigentiformis*' from Craig-y-Cilau and some other crags in the Mynydd Llangattock area has a different peroxidase phenotype (C2 C3 (C4) E2 E3). It readily grows into a well developed tree, usually with rather more robust shoots. The leaves are somewhat more oblong in outline, and tend to be biserrate (Fig. 5j–o); the fruits are rather larger, subglobose (length/breadth ratio c. 0·85–0·95) and a brighter red. We have found material with this peroxidase phenotype and morphological characters on Carboniferous Limestone at Craig-y-Cilau and crags to the east on Mynydd Llangattock, in Cwm Clydach, and on Old Red Sandstone at Taren-yr-Esgob, Daren Lwyd and near Cwmyoy in the Black Mountains. Dr Q. O. N. Kay has obtained chromosome counts of 2n = 68 in plants from Cwm Clydach (v.c. 41) and Daren Disgwylfa (v.c. 42). The population at Taren-yr-Esgob has leaves with a more narrowly cuneate base and sharper and more deeply incised teeth (Fig. 5m). The leaf-shape difference appears to be correlated with a consistently clearer separation between peroxidase bands E2 and E3 in this population than elsewhere, but both differences are rather slight.

(c) A morphologically uniform population of rather small trees in the Avon Gorge shows consistently the peroxidase phenotype C2 (C3) (E2) E3. In leaf shape (Fig. 5p) and habit this plant could be mistaken at first sight for *S. porrigentiformis*, but it has lighter green leaves (usually 146A on the R.H.S. Colour Chart) which more nearly resemble a small *S. aria*. The Bristol '*porrigentiformis*' discussed by Proctor *et al.* (1989) is this plant.

(d) Plants on Seven Sisters Rocks near Symonds Yat in the Wye Valley, growing with *S. porrigentiformis* and showing a general resemblance to it in leaf-shape (Fig. 5q–s), habit, and fruit shape and colour have the peroxidase phenotype C1 C2 (C3) E1 E2; several morphologically different groups of individuals differ in the relative intensity of the bands. Similar phenotypes occur in *S. eminens* from the same area, and appear to be common in crimson-fruited forms of *S. aria* sensu lato, in the Wye Valley generally. These plants cannot be genetically identical with any of the other *S. porrigentiformis*-like populations we have examined.

The very widely distributed *S. rupicola* (Syme) Hedl. is rather sporadically scattered in our area. Samples examined from Gower, Craig-y-Cilau and Craig Breidden agree in peroxidase phenotype with material from Devon, Yorkshire and Scotland (Proctor *et al.* 1989 and unpublished data).

ANOMALOUS INDIVIDUALS

We have not searched systematically for aberrant individuals within otherwise uniform apomictic populations, but a few examples have come to light in the course of our sampling. One individual at the top of Craig-y-Rhiwarth, in a population mainly of *S. leptophylla* with a few *S. porrigentiformis* (type (a) above), has distinctive ovate leaves and gave a peroxidase phenotype (C2 E1 E3) different from either. A tree below Leigh Woods, Bristol, with long cuneate-based many-veined leaves, clearly differing from *S. aria* or any of the named apomicts, also has a unique peroxidase phenotype. A single tree with rather narrow rhomboid leaves at Cwmyoy gave a peroxidase phenotype similar to but not identical with *S. wilmottiana*.

DISCUSSION

Our results are consistent with accepted taxonomic views for the more geographically restricted apomictic species, namely *S. minima*, *S. leyana*, *S. bristoliensis*, *S. leptophylla* and *S. wilmottiana*. The peroxidase isoenzyme variation confirms that *S.* × *vagensis* is probably a sporadically occurring sexual hybrid. However, the most interesting findings relate to *S. eminens* and *S. porrigentiformis*.

The isoenzyme evidence confirms the difference between *S. eminens* from the Avon Gorge and material from the Symonds Yat area (Fig. 6). Indeed the difference in peroxidase phenotype suggests that the two populations may not be very closely related. On the other hand, the peroxidase evidence links the Avon Gorge form with trees on Mendip, with the population that has been named *S. porrigentiformis* on the Menai Straits, and with *S. hibernica*. Warburg verbally suggested an affinity between a specimen from Cheddar and *S. hibernica*, without identifying it with that species (P. J. M. Nethercott, in litt.). These plants all show similarities in leaf form and toothing, and in growth habit, and their relationships need further investigation.

Our observations on *S. porrigentiformis* and related plants show why there have been problems in delimiting this species in South Wales, and suggest how these may be resolved. The widespread plant (type (a) above; Fig. 7) corresponds to the generally accepted concept of *S. porrigentiformis* (Warburg 1952, 1957; Butcher 1961) and appears identical with the Wye Valley specimen on which Warburg typified this species (Offa's Dyke, Tidenham, 18 September 1933, *A. J. Wilmott (no. 4484)* (**BM**)). It is locally accompanied or replaced in the Mynydd Llangattock-Cwm Clydach area and the Black Mountains by genetically distinct populations (type (b); Fig. 8) which should be regarded as an independent taxon. The uniform but probably more local plant in the Leigh Wood quarries (type (c)) needs further study in the context of other Avon Gorge, Mendip and Wye Valley populations.

Warburg & Kárpáti (1968) associate *S. porrigentiformis* with *S. graeca* (Spach) Kotschy rather than with *S. aria* sensu stricto. The *S. porrigentiformis*-like plants which accompany true *S. porrigentiformis* near Symonds Yat are clearly genetically different from any we have examined elsewhere, but they share *S. graeca*-like characters (cuneate-based obovate leaves and crimson subglobose fruits with few lenticels) with *S. porrigentiformis* and a number of our other apomicts. Field observations and herbarium material both indicate the existence of much variation in the Wye Valley. In South Wales, as in South-west England, the peroxidase variation in *Sorbus* seems nicely matched to the morphological variation and to the needs of recognizing and delimiting the apomictic populations. In the Symonds Yat area it appears that this is not so, and that considerable morphological variation may be accompanied by little or no variation in the peroxidase enzymes, especially among the more *S. graeca*-like plants. In general, if two individuals show different isoenzyme phenotypes under the same conditions, they cannot be genetically identical, but the fact that two individuals are identical with respect to a particular enzyme system does not necessarily

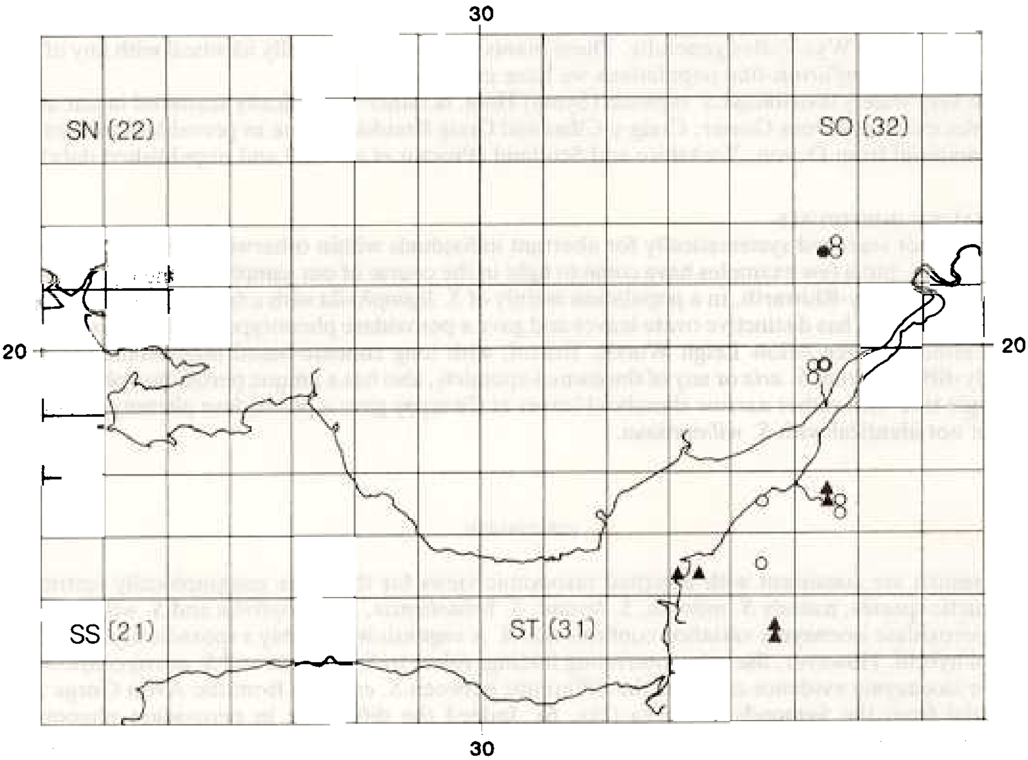

FIGURE 6. Distribution of *S. eminens* E. F. Warb. in 2-km squares (tetrads) of the National Grid. ● Symonds Yat-type peroxidase phenotype; ▲ Avon Gorge-type peroxidase phenotype; ○ other records of *S. eminens* sensu lato. The **O** shows the locality of the holotype specimen.

mean that they are identical in other respects. More work is needed on the Wye Valley populations, and exploration of other enzyme systems may well prove useful in this.

The apomictic *Sorbus* species we have considered are all confined to crags and rocky ground, an essentially disjunct habitat. Their present distribution must reflect an interplay between colonization and extinction on these 'islands' in a 'sea' of country they cannot colonize (Macarthur & Wilson 1967). *S. rupicola* has by far the widest total range (Perring & Sell 1968), in which wide disjunctions suggest fragmentation of a once more continuous area, perhaps in the more open landscape of the early Post-glacial (Pigott & Walters 1954; Birks 1973; Boyd & Dickson 1987). Next most widespread are *S. porrigentiformis* and *S. anglica*, both with much more coherent distributions centred on the South Wales limestone. Some of the more restricted distributions may have relic features, but to a great extent we are probably looking at rather recent patterns of bird dispersals (compare the patterns in *Rubus* of Weber (1987)) from centres of origin concentrated in three main areas, the Avon Gorge and Wye Valley, the Mynyd Llangattock area, and the Exmoor coast. From the peroxidase data, it is tempting to speculate that *S. porrigentiformis* was involved in the origin of *S. anglica*, *S. leyana*, *S. minima*, *S. bristoliensis* (Sell 1989) and other apomictic populations within its area (but excluding *S. leptophylla* and the North Devon apomicts); farther north, *S. rupicola* was probably the *S. aria*-group parent of *S. arranensis* and *S. pseudofennica* (Proctor *et al.* 1989). However, the inheritance of peroxidases in *Sorbus* is unknown, and likely to be complex (Gottlieb 1981), so these are no more than tentative conjectures which should stimulate search for other evidence.

It was Linnaeus's precept that the first step in understanding is to know the entities one is dealing with. However, the interest of *Sorbus* only begins with the delimitation and enumeration of apomictic microspecies. A far more interesting challenge is to understand how an apomictic group

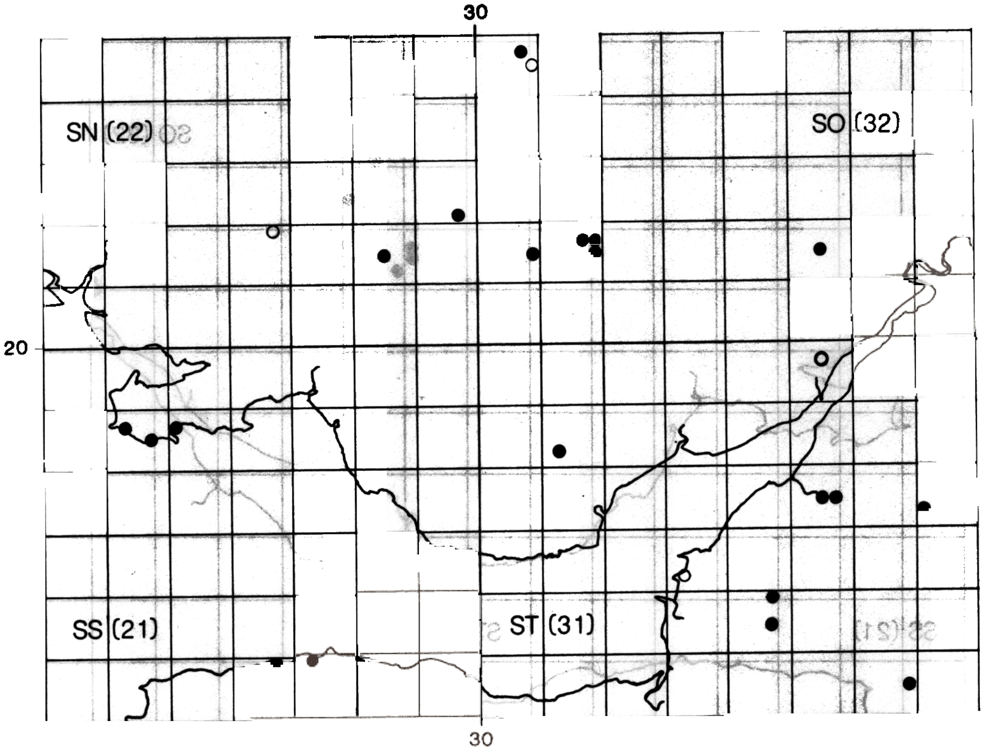

FIGURE 7. Distribution of *S. porrigentiformis* E. F. Warb. in 2-km squares (tetrads) of the National Grid. ● peroxidase phenotype (a); ○ tetrads from which we have seen material which on morphological characters appears certainly to be this type. **O** shows the location of the holotype specimen. Outside the area of this map, *S. porrigentiformis* confirmed as peroxidase phenotype (a) occurs in v.c. 3 in tetrads SY82.70, 92.62 and 92.64.

of this kind came into being, under what selection pressures, and how it functions over an extended span of time (Gustafsson 1947; Clausen 1954; Asker 1979). In this quest, fast-growing herbaceous plants (e.g. *Taraxacum* (Richards 1970a, b, 1973; Ford 1981)) and the long-lived populations of *Sorbus* offer complementary opportunities. In the latter genus, many questions of cytogenetics, population biology and ecology invite investigation, both in the apomictic populations of South Wales and South-west England, and in the mixed sexual and apomictic populations of the Wye Valley, Avon Gorge and Mendip which may well provide models for the kind of situation in which many of our present-day *Sorbus* apomicts originated.

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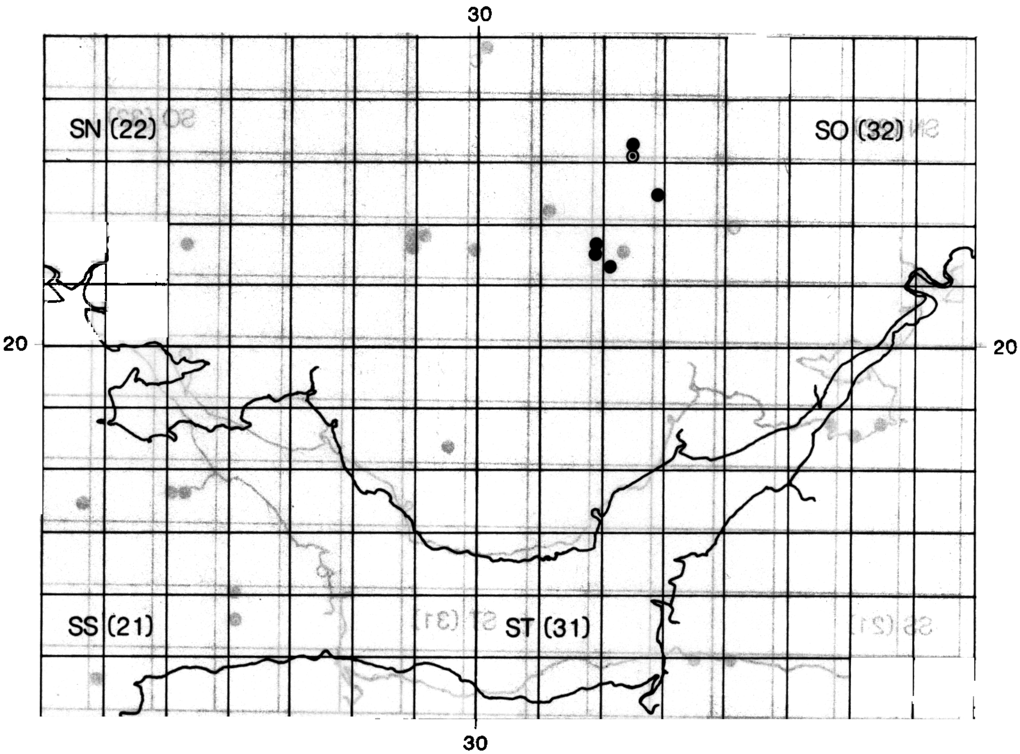

FIGURE 8. *S. porrigentiformis* sensu lato. Distribution of peroxidase phenotype (b) ('large-leaved *porrigentiformis*') in 2-km squares (tetrads) of the National Grid. ⊙ population at Taren-yr-Esgob.

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.PPENDIX

The table below gives the C.I.E. coordinates of the shades from the *R.H.S. Colour Chart* used in matching fruit colours for Table 1, and the corresponding colour names from the earlier *Horticultural Colour Chart* (British Colour Council 1938). The first two figures of the C.I.E. coordinates define the chromaticity (hue and saturation) of the colour on a modified colour triangle; the third coordinate measures percentage reflection. Colours 28A–33A appear in the 'orange-red group' and colours 44A–53A in the 'red group' of the *R.H.S. Colour Chart*; 45A is a nearly pure red. For further explanation see Royal Horticultural Society (1966).

Number in R.H.S. Colour Chart	Colour name	C.I.E. coordinates x	y	Reflection factor (%)
28A	Persimmon Orange	0·547	0·391	45·5
32A	Indian Orange	0·561	0·370	27·6
33A	Capsicum Red	0·567	0·355	23·6
44A	[unnamed]	0·592	0·339	14·6
45A	Guardsman Red	0·593	0·315	11·9
46A	Currant Red	0·546	0·310	9·4
53A	Cardinal Red	0·522	0·298	8·3