One-way introgressive hybridisation between *Sorbus aria* and *S. torminalis* (Rosaceae) in southern Britain

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ABSTRACT

Material of *Sorbus aria*-like plants from the Wye Valley with acutely-lobed leaves has been investigated using comparative morphology and reproductive fertility, which show that at least some such plants are *S. aria* introgressed with *S. torminalis*. The introgression was found to occur only from *S. aria* into *S. torminalis*. The primary and introgressed hybrids have lower pollen and fruit fertility than the parents. The parents show widespread overlap in distribution in southern Britain but introgression has been confirmed only for the Wye Valley. *Sorbus* × *vagensis* should be treated as a hybrid, not as a species.

KEYWORDS: Fertility, morphology, pollen, *Sorbus latifolia*, *Sorbus* × *tomentella*, *Sorbus* × *vagensis*.

INTRODUCTION

The *Sorbus latifolia* (Lam.) Pers., Broad-leaved Whitebeam aggregate comprises taxa which have arisen by hybridisation between *S. torminalis* (L.) Crantz, Wild Service-tree, and members of the *S. aria* (L.) Crantz, Common Whitebeam aggregate (Warburg 1962; Sell 1989; Nelson-Jones *et al.* 2002). They are characterised by having leaves with triangular, acute or acuminate lobes and greenish-grey tomentum below, and large fruits which are brown, orange or yellow when ripe. In Britain, the *S. latifolia* aggregate was first separated by Syme (1875, as *Pyrus latifolia* Syme), and now contains seven taxa (Sell 1989), six of which are apomictic polyploids (*S. bristoliensis* Wilm., *S. croceocarpa* P. D. Sell, *S. decipiens* (Bechst.) Irmisch, *S. devoniensis* E. F. Warb., *S. latifolia* sensu stricto and *S. subcuneata* Wilm.), and the other is the primary diploid hybrid *S.* × *vagensis* Wilm.

When he first described it, Wilmott (1934) considered that *S.* × *vagensis* might be *S. torminalis* × *anglica* Hedl. or × *porrigentiformis* E. F. Warb., and suggested it grew true from seed after noting the morphological uniformity of a cluster of trees a little south of Symonds Yat top. He chose the epithet to reflect the occurrence of the hybrid in the Wye Valley (of the river Wye or *flumen Vaga*). Warburg subsequently found that the uniformity noted by Wilmott was due to suckering rather than reproduction from seed (Riddelsdell *et al.* 1948), and he treated it as a variable, diploid hybrid between *S. aria* and *S. torminalis* (Warburg 1952), which is now its accepted parentage. It is now known to have arisen a number of times independently, with *S. torminalis* as the female parent (Proctor & Groenhof 1992; Lemche 1999; Fay *et al.* 2002; Chester *et al.* 2007). Sell (1989) treated *S.* × *vagensis* as a species rather than a hybrid since British material did not match in morphology continental material of the same parentage; we follow his nomenclature here but not his concept of the taxon as a species.

During a series of *Sorbus* surveys of cliffs in the Wye Valley in 2000–2003 commissioned by English Nature (now Natural England), L. Houston, C. Charles and A. C. Tillotson repeatedly collected forms of *S. aria* with acutely-lobed leaves (Houston *et al.* 2001, 2002, 2003, 2004; Figure 1a, b). In exasperation at the absence of any name to call them, they were nicknamed *Sorbus* “Yet another form” by C. Charles. These plants were shown to T. Rich, who, after much discussion, began to suspect these might be *S. aria* introgressed with *S. torminalis*, not previously reported from Britain but known from the continent (Chabert 1906; Aas *et al.* 1994; Oddou-Muratorio *et al.* 2001).

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TABLE 1. CHARACTERS DISTINGUISHING *SORBUS ARIA*, *S. TORMINALIS* AND THEIR PRIMARY DIPLOID HYBRID *S.* × *VAGENSIS,* COMPILED FROM THE LITERATURE (E. G. WARBURG 1962, CHALLICE & KOVANDA 1978) AND PERSONAL OBSERVATION

	Sorbus aria	*Sorbus* × *vagensis*	*Sorbus torminalis*
Habit	No suckering	Weakly suckering	Strongly suckering
Petiole length	7–24(–29) mm	(15–)20–35(–43) mm	(15–)20–50(–58) mm
Leaf shape	±Orbicular, ovate, elliptical or oblong (rarely obovate), (1·0–)1·1–2·0(–2·4) times as long as wide	Ovate, elliptical, oblong or rhombic-elliptical, (0.8–) 1·0–1·5(–1·9) times as long as wide	Ovate, 0·8–1·3(–1·5) times as long as wide
Leaf veins	(6–)9–14(–15) pairs	6–10(–12) pairs	(3–)4–6(–7) pairs
Leaf pubescence at maturity	White tomentose below	Greenish-grey tomentose below, sometimes subglabrous	± Glabrous below
Leaf apex	Obtuse to acute	Acute or subacute	Acuminate
Leaf base	Truncate to rounded (rarely cuneate or cordate)	Rounded or cuneate	Rounded, truncate or cordate, rarely broadly cuneate
Leaf lobing	Unlobed or with shallow broadly rounded lobes to 1/6 way to midrib	Shallow lobed with acute or acuminate lobes to ¼ way to the midrib	Deeply lobed with triangular, acute or acuminate lobes to ½ (rarely all) way to the midrib
Leaf margin	Doubly crenate-serrate, teeth with one side a little longer than the other	Finely serrate with small somewhat appressed teeth	Finely serrate with small strongly asymmetric appressed teeth
Inflorescence	Densely crowded	Crowded	Lax
Sepals	Eglandular	Sparsely glandular	Glandular
Styles	2–3, free, lanuginous at base	2–3, variably joined up to half way, lanuginous at base	3, joined up to ½–⅔way, glabrous at base
Fruit colour	Red	Yellow, orange or brownish-orange	Brown
Lenticels on fruits	Few to medium, small to medium lenticels, sometimes large ones	Medium to numerous, small and medium lenticels	Numerous small lenticels and some large ones
Fruit length	(9–)10–15(–16) mm	(9–)10–17 mm	(9–)10–17(–18) mm

In this paper we present the results of morphological and reproductive biology investigations into these Wye Valley *S. aria* plants with acutely-lobed leaves. *Sorbus aria*, *S. torminalis* and *S.* × *vagensis* can be readily separated morphologically using many characters (Table 1), and putative backcrosses might be expected to show some characters intermediate between *S.* × *vagensis* and *S. aria*, such as relatively long petioles, few pairs of veins and greener undersides to the leaves.

Hybrids are often sterile or show reduced fertility compared to their parents. In order for back-crossing to occur, some of the primary hybrids and backcrosses must produce at least some fertile pollen and/or seeds. The primary hybrids were reported as either sterile or fertile in France (de Poucques 1951), but this has not been studied in Britain so the relative fertility of the taxa has been investigated from pollen and fruit.

We have also compiled information on the distribution of *S.* × *vagensis* and the locations where its parents occur together to see how widespread back-crossing might potentially be in Britain.

METHODS

COMPARATIVE MORPHOLOGY

Herbarium material of *S. aria* (21 samples), *S. torminalis* (18 samples), *S.* × *vagensis* (19 samples) and putative backcrosses of *S.* × *vagensis* with *S. aria* (13 samples) were selected from **NMW** (Appendix 1). Material was selected from the Wye Valley and from elsewhere in Britain where hybrids are unknown. Some material previously investigated for DNA analysis (Fay *et al*. 2002) was also selected (marked in Appendix 1). The following set of eight characters were selected from the most important characters found by Aas *et al*. (1994), with the addition of lobe shape:

1. petiole length.
2. lamina length.
3. lamina width.
4. lamina width at 0·9 of the leaf length.
5. shape of lamina base (scored as: 0 cordate, 1 weakly cordate, 2 truncate-cordate, 3 truncate, 4 broadly cuneate, 5 rounded, 6 rounded-cuneate, 7 cuneate).
6. number of pairs of veins (note: strictly speaking these are not true pairs).
7. depth of incision of deepest lobe (measured in direction of veins usually on the lowest or second lowest lobe from the base).
8. shape of largest lobe apex (scored as: 1 acuminate, 2 narrowly acute, 3 broadly acute, 4 narrowly obtuse, 5 broadly obtuse, 6 rounded, 7 not lobed).

Two leaves from the short lateral vegetative shoots, excluding the oldest and youngest leaf (Aas *et al*. 1994), were scored for each character. The data were analysed using Principal Components Analysis in 'PAST' version 1.27 (Hammer *et al*. 2001), with data normalised by division by the standard deviations.

POTENTIAL FERTILITY

Potential pollen viability was investigated using Alexander's Stain (Alexander 1969) which allows differentiation between unviable and potentially viable pollen. True pollen viability can be assessed by germinating fresh pollen, but this cannot be done with herbarium specimens. Unfortunately it was only rarely possible to use the same material for pollen analysis as for morphological analyses as material collected at flowering time often lacks mature leaves from the short shoots.

Anthers were removed from herbarium specimens with tweezers under a low-power binocular microscope, and placed onto a slide with a drop of Alexander's Stain, warmed briefly on the hotplate, then broken up with the tweezers to release the pollen. The preparation was then covered with a cover slip and replaced on the hotplate to improve the uptake of the stain. The slides were then examined under a high-power compound microscope for areas of dense pollen grains. A minimum of 50 grains were counted where possible. Potentially viable grains were counted as those which were large and rounded-triangular with cell walls which stained green and had cytoplasm inside which stained uniformly bright red. Small deformed grains or those staining green only with very little or no red staining inside (i.e. no cytoplasm) were considered infertile. Repeat samples were taken from five specimens to assess the reliability of the method. The mean difference between samples was 14%, ranging from 2–23%; overall means are therefore more likely to be reliable than individual samples.

In 2004, an excellent fruiting year, 30 fruits were collected from trees of *S. aria*, *S. torminalis*, *S.* × *vagensis* and putative backcrosses in the Wye Valley, Buckinghamshire and the Avon Gorge and assessed for seed content. The fruits usually contain both large, plump, fertile seeds rather like apple pips, and smaller flat seeds which seem to consist only of a seed coat which had some development but then aborted. Some fruits were subsequently found to contain only aborted seeds and were not included. It was found that extraction of the seeds from *S. torminalis* fruits and to some extent from *S.* × *vagensis* fruits was considerably easier from fruit bletted in the fridge for a few months than from fresh fruit.

DISTRIBUTION OF TAXA

Records of *S.* × *vagensis* were compiled from herbaria (**BEL**, **BIRA**, **BIRM**, **BM**, **BRISTM**, **CGE**, **E**, **GL**, **GLAM**, **K**, **LDS**, **LTR**, **MANCH**, **NMW**, **OXF**, **RNG** and **UPS**), published and unpublished literature and reports, and from correspondence with botanists.

For comparison of the distribution of *S.* × *vagensis* with its parents, data were collated from existing databases and floras to investigate where *S. aria* and *S. torminalis* occur together. Hectad data were extracted from the *New Atlas* (Preston *et al*. 2002). Tetrad (2 × 2 km square) data were taken from local county floras for vice-counties where *S. aria* is considered native in Stace *et al*. (2003). Tetrads where both species were recorded were extracted and no distinction was made between alien and native sites within the vice-counties, although some records are clearly of planted trees. Unpublished data for Buckinghamshire were supplied by R. Maycock, Berkshire data by M. Crawley, Gloucestershire data by M. A. R. and C. Kitchen (the data were noted as incomplete) and Monmouthshire data by T. G. Evans.

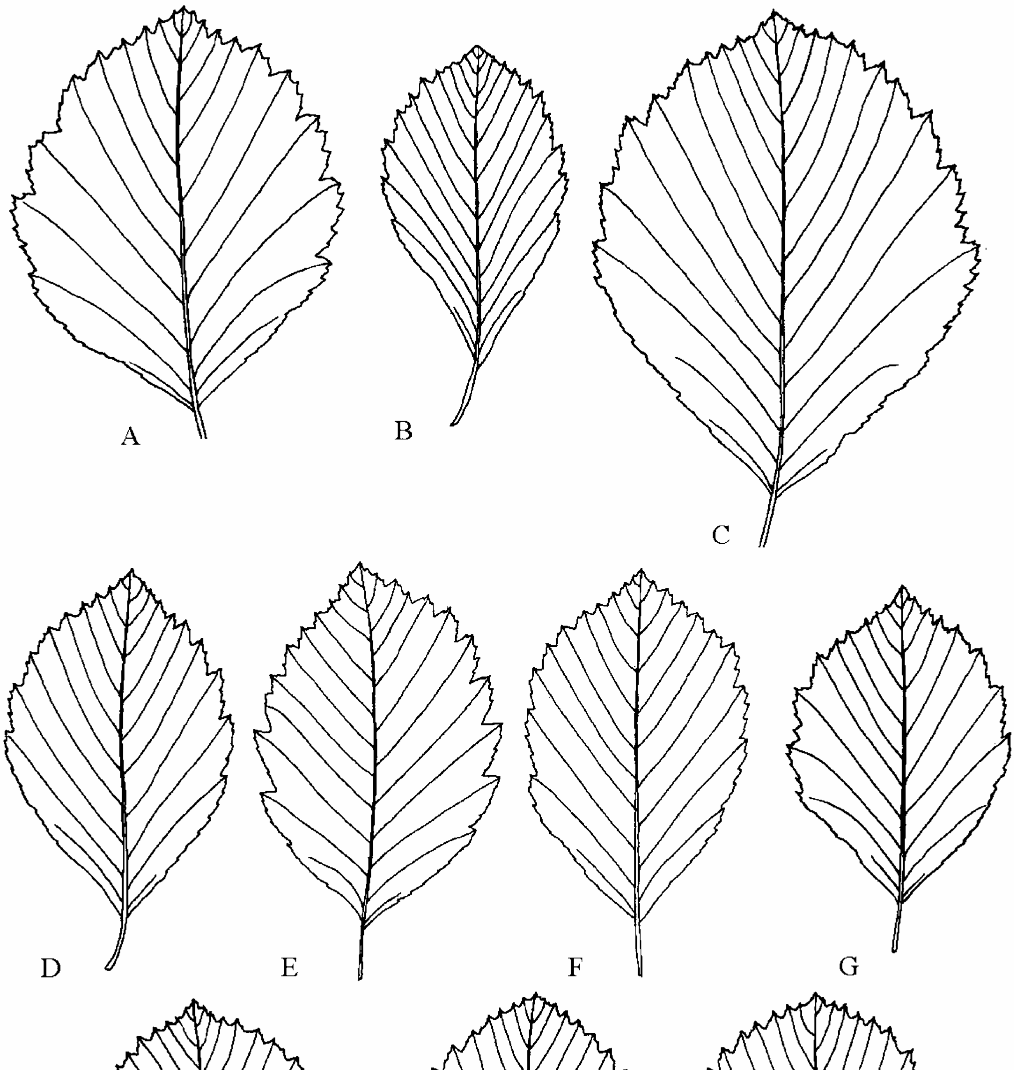

FIGURE 1. Putative *S. aria* × *S.* × *vagensis* backcrosses. A, Ban-y-gor rocks (V.2001.13.37). B, Ban-y-gor rocks (V.2002.17.108). C, Rosemary Topping (Sample 1). D, Gorrashill (Sample 11). E, Pinnacle of Pinnacles, Great Doward (Sample 39). F, Seven Sisters (Sample 40). G, Seven Sisters (Sample 59). H, Symonds Yat (Sample 62). I, Wintour's Leap (Sample 75). J, Wintour's Leap (Sample 77). Scale bar = 1 cm. Del. T. C. G. Rich.

RESULTS

COMPARATIVE MORPHOLOGY

Figure 1 shows variation in lobing of leaves of putative *S. aria* × *S.* × *vagensis* backcrosses; for comparative illustrations of *S. aria*, *S. torminalis* and *S.* × *vagensis,* see Fay *et al.* (2002). The variation is presumably due to differences in parentage.

The Principal Components Analysis plot for Components 1 and 2 is shown in Figure 2. Component 1 had an Eigenvalue of 4·33 and accounted for 54·5% of the variance. Component 2 had an Eigenvalue of 1·79 and accounted for 22·5% of the variance. The Joliffe cut-off value, an informal indication of the value below which components may no longer be considered significant, was Eigenvalue 0·7, suggesting that the third Component was of minor importance. All eight characters had significant loadings in Component 1 (unsurprising in that they had all been selected as important), with the depth of incision, number of veins and petiole length being the most important (in that order). The main loadings in Component 2 were leaf length, leaf width and width at 0·9 of the length.

Figure 2 shows *S. torminalis* is clearly separated from the other taxa by Component 1. *Sorbus* × *vagensis* is intermediate between *S. torminalis* and *S. aria*, as might be expected (though Sell 1989 regarded the leaf morphology as nearer to *S. torminalis* than to *S. aria*). A few *S.* × *vagensis* samples showed minor overlap with *S. aria*; one was of shaded leaves from the tree at Cheddar Wood, and the other a somewhat atypical form from Lady Park Wood with narrow obovate leaves rather like *S. subcuneata* (see Sell 1989, page 389). Plants with acutely-lobed leaves ascribed to the possible backcross of *S.* × *vagensis* with *S. aria* were located between *S. aria* and *S.* × *vagensis*, overlapping more with *S. aria* but showing less scatter. The greater overlap with

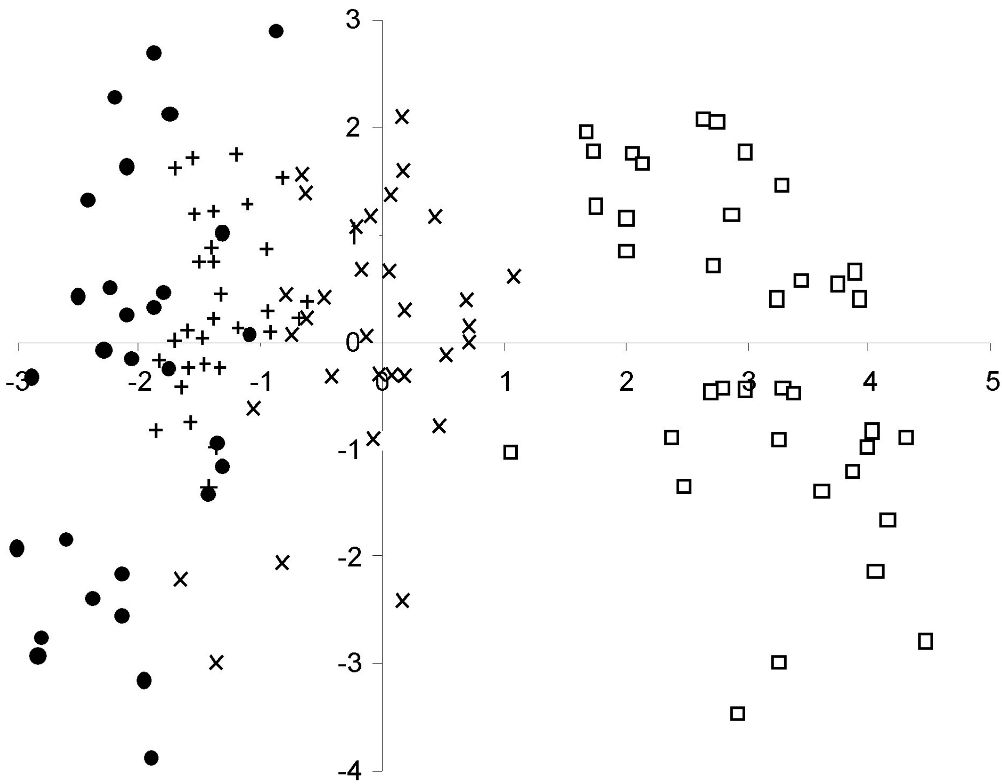

FIGURE 2. Principal components analysis of *Sorbus* taxa. ● *S. aria*; □ *S. torminalis*; × *S.* × *vagensis*; + possible backcrosses between *S. aria* and *S.* × *vagensis*.

TABLE 2. POTENTIAL POLLEN VIABILITY ON *SORBUS* ASSESSED USING ALEXANDER'S STAIN. (DATA IN PART COURTESY A. KARRAN AND J. ROGERS)

Species	Locality	NMW accession number	Percentage fertile
S. aria	Bix (v.c. 24)	23.94.1258	92
	Box Hill (v.c. 17)	83.6.480	56
	Buckingham (v.c. 24)	78.35.4800	73
	Cheddar Gorge (v.c. 6)	29.190.2	99
	Clevedon (v.c. 6)	49.29.1759	74
	Conkwell (v.c. 7)	28.131.2922	33
	Godstone (v.c. 17)	V.94.24.7521	67
	Horsley (v.c. 17)	V.2000.34.64	86
	Leigh Woods (v.c. 6)	25.12.1	100
	Nightingale Valley (v.c. 6)	25.149.10666	78
	Nuffield (v.c. 23)	V94.62.599	99
	Princes Risborough (v.c. 24)	V.94.24.1466	98
	Reigate (v.c. 17)	23.94.1256	23
	Sea Walls, Durdham (v.c. 34)	(fresh material)	97
	Tutshill (v.c. 34)	28.131.2924	100
		Mean	**78**
S. torminalis	Abergele (v.c. 50)	30-609-12	82
	Afon Arth, Cards. (v.c. 46)	76-68B-11	83
	Bewdley (v.c. 34)	42-138-311	89
	Castle Coch (v.c. 41)	2001-025-003	65
	Chepstow (v.c. 35)	28-131-2949	100
	Exeter (v.c. 3)	22-289a-123	92
	Hampstead (v.c. 21)	26-540-128	90
	Lawrenny (v.c. 45)	76-42B-4	65
	Monmouth (v.c. 35)	35-435-48	92
	Much Marcle (v.c. 34)	23-94-1250	46
	Newlyn (v.c. 1)	25-149-10649	98
	Overton-Chirk (v.c. 40)	94-24-1462	90
	Pen Moyle (v.c. 34)	No number	50
	Sandy Haven (v.c. 45)	72-137B-8	66
	Stafford (v.c. 39)	No number	96
	Symonds Yat (v.c. 34)	49-29-1765	78
		Mean	**75**
S. × vagensis	Bicknor Walks (v.c. 34)	25.149.10659	25
	Gorrashill (v.c. 35)	V.2004.3.100	29
	Symonds Yat (v.c. 34)	28.131.2903*	0
	Symonds Yat (v.c. 34)	28.131.2939	0
	Symonds Yat (v.c. 34)	28.131.2941	5
	Symonds Yat (v.c. 34)	25.149.10652*	0
		Mean	**10**
putative backcross	Symonds Yat (v.c. 34)	V.2004.3.111	35

* possible duplicate collections from the same plant

S. aria might be expected as plants might be F2, F3 or further backcrosses with *S. aria*. These PCA results are very similar to those of Aas *et al*. (1994) for Swiss material.

POTENTIAL FERTILITY

Table 2 lists the potential pollen viability of the taxa studied using Alexander's Stain. Both parents had quite high mean potential pollen viability (*Sorbus aria* mean 78% and range 23–100%, *S. torminalis* mean 75% and range 46–100%), but viability was much lower in *S.* × *vagensis* (mean 10%, range 0–29%). The one putative backcross studied had 35% pollen viability, higher than *S.* × *vagensis,* but still low compared to *S. aria* and *S. torminalis*.

Fruits were present on all the *S.* × *vagensis* and putative backcrosses investigated in the Wye Valley in 2004. The number of fruits produced varied between trees, for instance some *S.* × *vagensis* trees produced copious quantities of fruit but others only small numbers, though whether this is due to inherent differences in fertility or variation in pollination remains to be established. Table 3 lists the mean number of seed per fruit for the samples analysed. The parents *S. aria* and *S. torminalis* were the most fertile (overall mean 2·4 ± 0·104 s.e. and 1·9 ± 0·076 s.e. seeds per fruit respectively), *S.* × *vagensis* had lower fertility (overall mean 1·5 ± 0·064 s.e.) and the putative backcrosses lower fertility still (overall mean 1·2 ± 0·057 s.e.). A one-way analysis of variance shows that there are significant differences in fruit set among the four taxa ($F = 29·5$, 3 d.f., $P << 0·001$), and each pair is significantly different from each other with the exception of *S.* × *vagensis* and the putative backcrosses (Tukey test).

DISTRIBUTION OF TAXA

The records traced for *Sorbus* × *vagensis* are listed in Appendix 2 and are mapped at a tetrad level in Figure 3. This shows *S.* × *vagensis* is restricted in distribution from the Mendips to the Wye Valley, and has been recorded in about 16 sites in 13 tetrads in V.cc. 6, 34, 35 and 36, principally concentrated on the Wye Valley. It occurs on open rocks, cliffs, scrubby woodland and in tall woodland, almost always on Carboniferous Limestone and associated soils, associated with *Fraxinus excelsior*, *Tilia cordata*, *Taxus baccata* and other *Sorbus* species including both its parents.

A comparison of the maps of *S. aria* and *S. torminalis* in the *New Atlas* (Preston *et al.* 2002) shows that they overlap extensively in distribution in southern England and Wales, being jointly present in over 160 hectads, which suggests the possibility of widespread hybridisation. However, as the hectad mapping scale is relatively crude, in many of these hectads *S. aria* and *S. torminalis* may not actually be growing together, especially as they

TABLE 3. NUMBER OF FERTILE SEEDS PER FRUIT FOR FERTILE FRUITS OF FOUR *SORBUS* TAXA COLLECTED IN AUTUMN 2004

Taxon	Locality	n	Mean no. seeds per fertile fruit (± s.e.)
S. aria	Leigh Woods	30	1·93 ± 0·11
	Great Doward	17	2·4 ± 0·25
	Yousden, Buckinghamshire	30	2·9 ± 0·16
S. torminalis	Leigh Woods	30	2·63 ± 0·17
	Near Ship Rock, Coldwell Rocks	27	1·67 ± 0·16
	Symonds Yat 261	27	1·37 ± 0·13
	Symonds Yat car park corner	30	1·63 ± 0·17
	Symonds Yat near toilets	30	2·5±0·21
	Symonds Yat, Bowlers Hole	30	1·73 ± 0·13
S. × *vagensis*	Biblins, Great Doward	30	1·53 ± 0·13
	Symonds Yat, car park corner	27	1·11± 0·08
	Symonds Yat, 260	23	1·65 ± 0·16
	Symonds Yat, row of 10	16	1·13 ± 0·09
	Symonds Yat, west of toilets	14	1·14 ± 0·1
	Needle Rock, Coldwell Rocks	30	2·1 ± 0·16
putative backcross	West of Ship Rock, Coldwell Rocks	27	1·15 ± 0·09
	Bowlers Hole	7	1·14 ± 0·14
	Symonds Yat, car park by rowan	24	1·25± 0·09

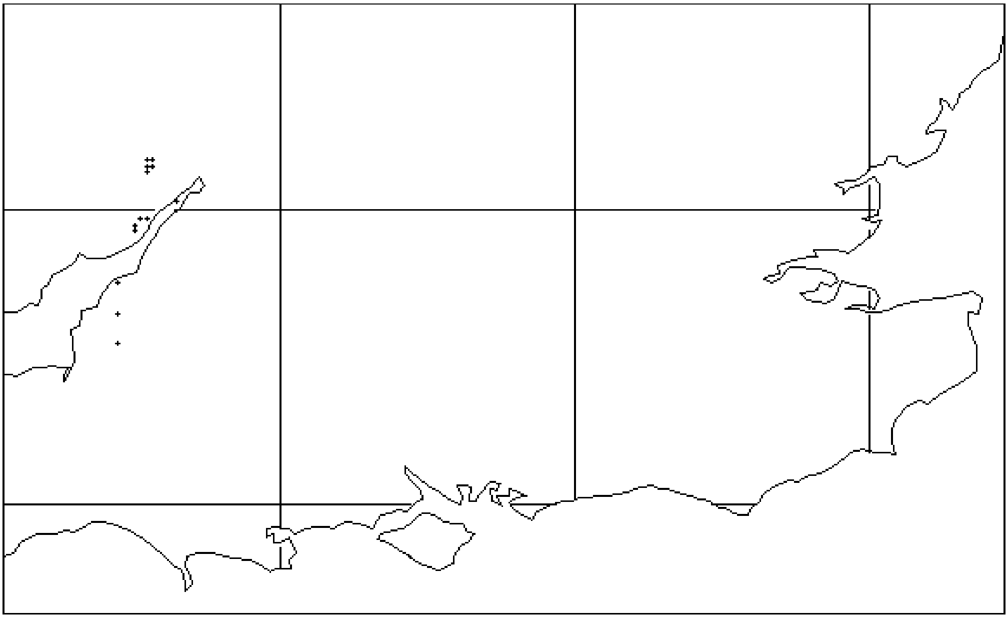

FIGURE 3. Tetrad distribution map of *Sorbus* × *vagensis*.

occupy different niches. *Sorbus aria* is most characteristic of open woods, scrub and hedges on calcareous soils over chalk and limestone, and is found more rarely on acidic soils. *Sorbus torminalis* is usually associated with ancient woodlands and hedgerows, and shows a marked preference for soils derived from clays and those developed over hard limestone (Roper 1993). Finer scale data were therefore compiled at the tetrad level for which there are ±comparable data across southern Britain, and Figure 4 shows tetrads in which *S. aria* and *S. torminalis* have both been recorded. This still does not necessarily indicate the two species are actually growing together, but gives a closer indication of where they are more likely to do so. This shows 149 tetrads scattered across southern Britain with clusters in the Wye Valley, the Mendips, Berkshire and the North Downs in Kent. Given this widespread occurrence of both species in reasonable proximity, it is perhaps surprising that the primary hybrid *S.* × *vagensis* is not more widely recorded, but we know relatively few sites where *S. aria* and *S. torminalis* grow intimately associated with each other. In a systematic survey of the central plateau of Switzerland, Rudow & Aas (1997) found the primary hybrid in 38 of the 160 sites investigated; it occurred in 35% of the sites where both parents were present, and 87% of its sites had both parents.

Putative backcrosses – identified from their morphology – were widespread in the Wye Valley (Appendix 1), and some similar plants were found in Cheddar in 2006 (L. Houston, pers. comm.). No clear backcross material has been seen from elsewhere in Britain.

DISCUSSION

The Principal Components Analysis (Figure 2) indicates that the Wye Valley plants with acutely-lobed leaves could be *S. aria* introgressed with *S. torminalis*. Morphologically, the backcrosses are easily separated from the primary *S.* × *vagensis* in having shorter petioles, much shallower lobes, whiter undersides of the leaves and red fruits. The clearer examples of backcrosses can be differentiated from *S. aria* by the combination of the acute lobes and greener undersides of the leaves. It is harder to be certain about the dividing line between pure *S. aria* and introgressed hybrids due to morphological variation in lobing of *S. aria* leaves. Variation in the extent of rounded lobes can be seen in many apparently pure *S. aria* populations (e.g. Bignor Hill, Sussex or Park Wood, Buckinghamshire; **NMW**), but plants with acutely-lobed leaves are less frequent and tend to occur only where *S. torminalis* grows frequently in the vicinity of *S. aria*. Preliminary phytochemical data support the occurrence of back-crossing

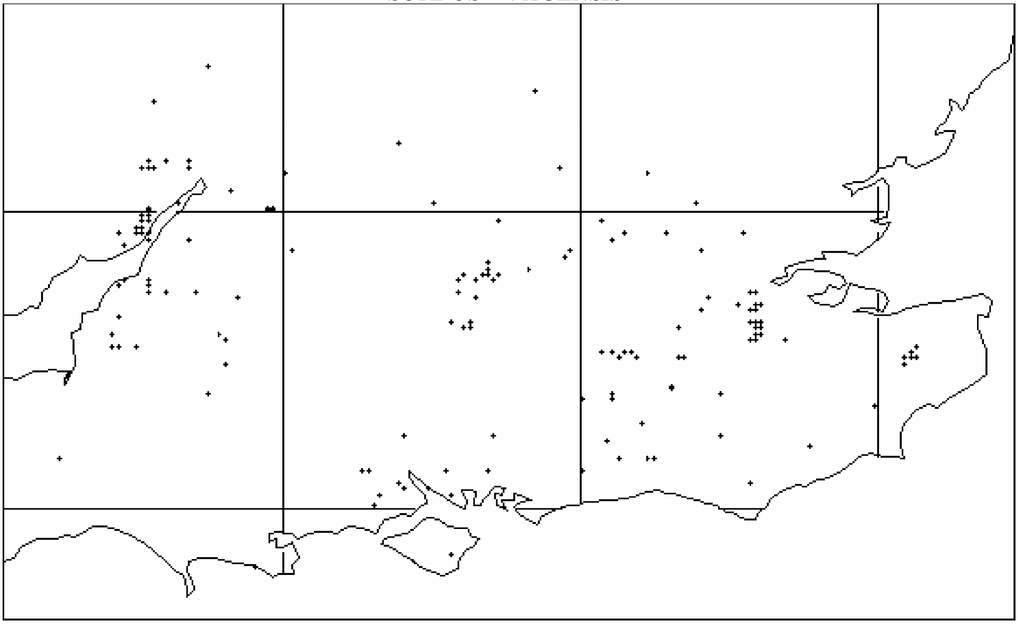

FIGURE 4. Tetrads in southern Britain in which both *Sorbus aria* and *S. torminalis* have been recorded.

(unpublished data), but further analysis requires a detailed molecular investigation.

The pollen tests suggest that at least some *S. × vagensis* trees and putative backcrosses have potentially fertile pollen, but that the fertility is an order of magnitude lower than that of the parents. Some trees had sterile pollen. All trees examined in 2004 had at least some fruit with well-formed seeds, with the hybrids having lower numbers of seeds per fruit than the parents, as might be expected. It is possible that all trees can act as mothers, or as both mothers and fathers, allowing continual introgression to occur. De Poucques (1951) suggested that when the hybrids have *S. aria* as the female parent they produce fertile fruits but when *S. torminalis* is the female parent they are sterile; this is inconsistent with our findings in the Wye Valley where *S. torminalis* is consistently the female parent (Chester *et al*. 2007) and *S. × vagensis* is fertile.

Given the large overlap in distribution of the parents in southern England, hybridisation is surprisingly rare, and so far introgressed hybrids have only been confirmed for the Wye Valley. There are other areas such as Surrey where *S. aria* plants with acutely-lobed leaves occur, and which could be relict from introgression at some stage in the past. *Sorbus × vagensis* has not been recorded in Surrey, but other *S. latifolia* aggregate taxa such as *S. croceocarpa* and *S. latifolia sensu stricto* are occasionally naturalised in that area and could be parents, although we have no evidence that this is so.

We conclude that introgression between *S. aria* and *S. torminalis* does occur in Britain. Backcrossing between *S. aria* and *S. torminalis* was first suggested for Britain by Riddelsdell *et al*. (1948) but they presented no evidence. Backcrossing has also been reported for Germany and Switzerland by Aas *et al*. (1994), and for France by Chabert (1906) and Oddou-Muratorio *et al*. (2001). Interestingly, like Aas *et al*. (1994), the introgression we have traced seems only to occur from *S. torminalis* into *S. aria* and not in the other direction and we have seen no material suggestive of back-crossing between *S. × vagensis* and *S. torminalis*. However, Oddou-Muratorio *et al*. (2001), from widespread sampling of French material, presented chloroplast DNA evidence showing that gene flow does occur from *S. aria* into *S. torminalis* albeit at a much lower rate than from *S. torminalis* into *S. aria*. Chabert (1906) gave a description of one plant from Fontainebleau he attributed to *S. latifolia × torminalis*. Use of such molecular methods and widespread sampling may show that gene flow occurs from *S. aria* into *S. torminalis* in Britain too.

There is now strong evidence that *S.* × *vagensis* behaves like many other hybrids, being diploid, of multiple origin, reduced fertility and back-crossing with one or both parents. We prefer to treat it as a hybrid as did Warburg (1952) and Stace (1997), and consider that Wilmott's (1934) and Sell's (1989) treatment of it as a species cannot be upheld.

Nomenclature of the hybrids may need to be updated. If *S.* × *vagensis* does not match continental material of *S. aria* × *torminalis* morphologically, as suggested by Sell (1989), then it might be worth retaining the name to label it separately. If *S.* × *vagensis* does match continental material of *S. aria* × *torminalis*, then *S.* × *vagensis* Wilm. becomes a synonym of *S.* × *tomentella* Gand. The name *S. latifolia* (Lam.) Pers. is often used for *S. aria* × *torminalis*, but Sell (1989) applied it to the widely cultivated, polyploid plant with broadly ovate leaves which can be consistently separated from *S.* × *vagensis* (at least in Britain). Further revision of the taxonomy of the hybrids should await a comparison of British *S.* × *vagensis* with continental *S.* × *tomentella* and *S. latifolia* sensu stricto and their ploidy level and reproductive mechanisms as French plants have been reported as either diploid or tetraploid, and as either fixed hybrids or not (de Poucques 1951, 1953; Dillemann & de Poucques 1954).

It may be useful to have a name for the introgressed plants, but there is no clear name available. Chabert (1906) described *S. aria* × *latifolia* from Fontainebleau as *S. latifolia* (Lam.) Pers. var. *ambigens* Chabert, and his brief description matches our plants from the Wye Valley with acutely-lobed leaves, though the parentage may be different. Plants with comparably lobed leaves have previously been reported from Britain under the names *S. incisa* (Rchb.) Hedl. or *S. aria* var. *incisa* Rchb. (Hedlund 1901, Marshall 1916, White 1912, Salmon 1930). Hedlund (1901) described *S. incisa* as similar to *S. aria* but having broadly elliptic leaves which were more lobed above, and he preferred to treat it as a species rather than accept a suggestion by Bechstein that it was only a form of *S. aria* which developed in fertile ground in the lowlands (*S. aria* sensu stricto being more a plant of the mountains). Examination of specimens determined as *S. incisa* in Hedlund's herbarium in Uppsala (**UPS**) reveals a range of British and continental *S. aria* material with ovate leaves and predominantly rounded lobes (as shown in Hedlund's 1901 Figure 33), or more rarely with acute lobes, and three incorrectly determined specimens of *S. anglica* Hedl. It is clear that Hedlund's concept is somewhat heterogeneous, and the name *S. incisa* is not clearly applicable to our Wye Valley plants with acutely-lobed leaves.

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APPENDIX 1. *SORBUS* MATERIAL USED FOR MORPHOLOGICAL ANALYSIS

NMW accession numbers are given, and * indicates material included in DNA study by Fay *et al*. (2002).

SORBUS ARIA

Bignor Hill (v.c. 13), V.2003.1.147; Bignor Hill (v.c. 13), V.2003.1.50; Blackdown (v.c. 13), V.2003.1.27; Bois de Garenne Sancere, Cher, France, V.2001.25.1129; Burnham Beeches (v.c. 24), V.2001.48.11; Coldwell (v.c. 34), V.2000.009.104*; Durford Heath (v.c. 13), V.2003.1.135; Durford Heath (v.c. 13), V.2003.1.136; Durford Heath (v.c. 13), V.2003.1.133; Gorrashill Wood (v.c. 35), V.2003.1.86; Great Doward (v.c. 36), V.2000.009.116; Laval en Laonnais, France, V.2001.25.1196; Lords Wood Quarry Great Doward (v.c. 36), V.2000.009.105*; Matlock (v.c. 57), V.1998.31.33; Mons en Laonnais, France, 85.40.6150; Naas (v.c. 34), V.2000.009.103*; Noar Hill (v.c. 12), V.2001.025.087; Pepperbox Hill (v.c. 8), V.2001.025.093; Pilgrim's Way, Clandon (v.c 17), 49.29.1757; Snoozin' Susie, Symonds Yat (v.c. 34), V.1999.033.528; Stane Street (v.c. 17), V.2003.1.144.

SORBUS TORMINALIS

Babel (v.c. 44), V.1999.012.25; Bangor (v.c. 49), 72.91B.10; Bois de Font Moreau, France, V.2001.25.1046; Bois de Roi Fontainebleau, France, V.2001.25.1184; Bontddu (v.c. 48), 73.60B.8; Cathays Cemetery (v.c. 41), V.2002.17.149; Coldwell Rocks (v.c. 34), V.2000.009.110*; Crawley Cliff, Oxwich (v.c. 41), V.2001.025.102; Cwmbach, Llanelli (v.c. 44), V.1999.008.41; Krivoklat, Bohemia, Czech Republic, V.2003.1.258; Lady Park Wood (v.c. 35), V.2001.025.040; Leigh Woods (v.c. 6), V.2001.025.294; Leigh Woods towpath (v.c. 6), V.2001.25.277; Llantrithyd (v.c. 41), V.2001.032.5; Naas (v.c. 34), V.2000.009.109*; Newbridge, Meifod (v.c. 47), V89.48.1; Saundersfoot (v.c. 45), V.2001.025.022; Wyndcliff (v.c. 35), V.2001.025.216.

SORBUS × *VAGENSIS*

Car park, Symonds Yat (v.c. 34), V.1999.033.541; Cheddar Wood (v.c. 6), V.1999.033.533; Coldwell (v.c. 34), V.2000.009.111*; Gorrashill Wood (v.c. 35), V.2003.1.84; Hedgeline Terrace, Symonds Yat (v.c. 34), V.2003.006.68; Lady Park Wood (v.c. 35), V.2004.011.37; Lady Park Wood (v.c. 35), 44.14.26; Lords Wood (v.c. 36), V.2000.009.112*; Lover's Leap (v.c. 35), V.2000.25.63; Naas (v.c. 34), V.2000.009.113*; Needle Rock, Coldwell Rocks (v.c. 34), V.1999.033.514; Nutwood, Ban y Gor (v.c. 34), V.2001.013.131; Symonds Yat (v.c. 34), 49.29.1775; White Wall waterpipe, Symonds Yat (v.c. 34), V.2003.6.53; White Wall, Symonds Yat (v.c. 34), V.2003.006.54; Wintour's Leap (v.c. 34), V.2004.011.30; Wintour's Leap (v.c. 34), V.2004.011.38; Wyndcliff (v.c. 35), 28.131.2898.

PUTATIVE BACKCROSS *S.* × *VAGENSIS* × *S. ARIA*

Bowlers Hole (v.c. 34), V.2003.006.81; Gorrashill Wood (v.c. 35), V.2003.1.85; Mounton Valley (v.c. 35), 28.131.2884; Pinnacle of Pinnacles, Great Doward (v.c. 36), V.2002.17.155; Rosemary Topping (v.c. 34), V.2003.1.88; Rosemary Topping (v.c. 34), V.2003.1.87; Seven Sisters (v.c. 36), V.2001.025.049; Seven Sisters (v.c. 36), V.2003.6.80; Seven Sisters, Great Doward (v.c. 36), V.2003.006.79; Symonds Yat Rock viewpoint (v.c. 34), V.2003.6.84; Symonds Yat West climbing area (v.c. 34), V.2003.6.82; Wintour's Leap (v.c. 34), V.2004.011.112; Wintour's Leap (v.c. 34), V.2004.011.113; Wintour's Leap (v.c. 34), V.2004.011.114.

APPENDIX 2. RECORDS OF *SORBUS × VAGENSIS*

V.C. 6, NORTH SOMERSET

Cheddar Wood (ST445550), one tree, McDonnell, E. J. & Rich, T. C. G., 28 October 1999, **NMW**.

King's Wood, Yatton (c. ST4564), at least two, well separated, coppiced trees in old woodland, Nethercott, P. J. M., 1984 (Willis 1984).

Weston Big Wood (c. ST4575), Archibald, J. F., 1968 (cf. Sell 1989); Nethercott, P. J. M., 1978, three trees (Willis 1978); Proctor, M. C. F., 10 June 1989, **NMW**; two large trees lost during storm of 25 January 2000, another damaged but regrowing, Nethercott, P. J. M., 1990 (Willis 1991). Not refound 2004.

V.C. 15, EAST KENT

[Blean Woods, Archibald, J. F., about 1959, *in litt.* to P. J. M. Nethercott (Willis 1978); unconfirmed.]

V.C. 34 WEST GLOUCESTER

Coldwell Rocks/Bicknor Woods/ Bicknor Walks/ English Bicknor (c. SO5615), Ley, A., 9 June 1874, **CGE**, **MANCH**; Bicknor Woods; Ley, A., 25 May 1875, **MANCH**; Watkins, B. M., June 1877, **MANCH**; Ley, A., 23 June 1877, **BEL**, **BIRA**, **E**; Watkins, B. M., October 1877, **BEL**, **BIRA**, **CGE**, **GLAM**, **MANCH**, **OXF**; Armitage, E., May and June 1888, **BRISTM**, **LTR**, **NMW**; Ley, A., 2 June 1888, 12 August 1891, 27 October 1892 and November 1892, **BEL**, **MANCH**, **UPS**; Armitage, E., October 1893 and May 1894, **BRISTM**; Ley, A., 12 May 1894 and 13 June 1899, **UPS**; Armitage, E., 24 August 1916 and July 1930, **BRISTM**, **NMW**; Roper, I. M., 17 August 1925, **LDS**; Warburg, E. F., September 1935, **BM**; Welch, B., 9 June 1939, **NMW**; Riddelsdell, H. J., 1941, **BRISTM** (Riddelsdell *et al.* 1948); Miles, B. A., 5 September 1956, **CGE**; Bishop, S. H. & M. S., 6 June 1992, **BRISTM**; Rich, T. C. G. & Houston, L., 4 October 1999; opposite Needle Rock; Rich, T. C. G., 30 June 2000, **NMW**; Charles, C., Houston, L. & Tillotson, A. C., September 2002, **NMW**; Rich, T. C. G. & Evans, T. G., 3 September 2003, **NMW**.

Highmeadow Woods (c. SO5413), Riddelsdell *et al.* (1948).

Staunton, woods near (c. SO5412), Ley, A., 28 June 1881, **CGE**, **MANCH** (Riddelsdell *et al.* 1948).

Symonds Yat (c. SO5615), Ley, A., June 1871, **CGE**; Ley, A., 12 August 1872, **E**; Purchas, W. H., August 1873, **MANCH**; Ley, A., 25 May 1875, **CGE**, **E**, **GLAM**, **K**; Bailey, C., 2 June 1882, **MANCH**; woods near, Ley, A., 12 Oct 1882, 26 May 1896 and 13 June 1899, **E**, **K**, **MANCH**, **NMW**, **OXF**; Shoolbred, W. A., 12 June 1901, **NMW**; Ley, A. & Armitage, E., May 1903, **BRISTM**; Bickham, S. H. & Ley, A., 8 June 1907, **CGE**; Ley, A., May 1909 and 6 June 1910, **K**, **UPS**; Anon., 4 September 1931, **BIRA**; Limestone rocks, Wedgwood, M. L., 10 June 1932, **BRISTM**; Wilmott, A. J., 18 September 1933, **UPS**; W. B., 4 November 1934, **UPS**; Vachell, E., August 1946, **NMW**; Burges, R. C. L., May 1948, **RNG**; Harris's Tea Garden, Mills, J. N., 2 August 1952, **MANCH**; limestone Woods, Tutin, T. G., 14 June 1953, **LTR**; Hyde, H. A., 11 August 1959, **NMW**; Sell, P. D. & Briggs, D., 29 September 1975, **CGE**; Below Symonds Yat Rock, Rich, T. C. G. & Kitchen, M. A. R., 18 September 1999, **NMW**; Below Symonds Yat Rock, Peregrine Pinnacle, east scrub south of Yat Rock, west side Yat Rock seven trees, White Wall and south-east corner of the view point, Charles, C., Houston, L. & Tillotson, A. C., September 2002, **NMW**.

Naas Cliff/Warren Grove (SO656027), Bishop, S. H., 8 July 1982, **BRISTM**; Rich, T. C. G., Kitchen, M. A. R. & C., 18 September 1999, **NMW**; Rich, T. C. G., 30 June 2000, **NMW**.

Ban-y-gor Rocks (ST544969 to ST546970), Charles, C., Houston, L. & Tillotson, A. C., September and October 2000, **NMW**.

Wintour's Leap (ST540965 to ST539965), Charles, C., Houston, L. & Tillotson, A. C., 1 September 2003, **NMW**.

V.C. 35 MONMOUTH

Cliff Wood, Mounton (c. ST5093), 1996, GL; 1 tree at north end of cliff, ST50764.94086, Rich, T. C. G., 6 October 2005, **NMW.**

Lady Park Wood (c. SO5414), Wade, A. E., 15 September 1943, **NMW**; Limestone cliff, Stace, C. A. / B.S.B.I. meeting, 18 September 1982, **LTR**; By the River Wye; SO546144, Houston, L., 12 September 2003, **NMW**; SO54694.14390, Rich, T. C. G., 6 October 2005, **NMW**.

Gorrashill Wood, Mounton (c. ST5093), Ley, A., 21 May 1891, **UPS**; Shoolbred, W. A., 21 May 1891, **NMW**; South-east side of a valley at Mounton; ST506936, Evans, T. G., 2 October 1995, **NMW**; Evans, T. G. & Rich, T. C. G., 3 September 2003, **NMW**.

Piercefield Cliffs (c. ST5296), Ley, A., 22 June 1878, **MANCH**; woods, Ley, A., 16 May 1894, **BRISTM**; Limestone rocks, Wilmott, A. J., 23 June 1932; near Temple Door, Wedgwood, M. L., 18 September 1933, **BRISTM**; Lover's Leap, Chepstow Park, ST522967, Evans, T. G., 1988, **NMW**.

Wynd Cliff (c. ST5297), Ley, A., 23 June 1873, **BIRM**; Shoolbred, W. A., 9 June 1878 and 25 June 1894, **BEL**, **NMW**; Bickham, S. H., 20 August 1903, **CGE**, **E**; Warburg, E. F., September 1935, **BM**.

V.C. 36, HEREFORD

Great Doward (c. SO5516), Watkins, B. M., 1880, **CGE**; Ley, A., July 1888, **BRISTM**; Warburg, E. F., September 1935, **BM**; one large tree, SO555151, Rich, T. C. G. & Houston, L., 9 October 2002, **NMW**.

Lord's Wood (c. SO5515), Ley, A., 11 June 1888, **CGE**, **NMW**; near The Biblins, three trees SO551145, Stace, C. A. / B.S.B.I. meeting 18 September 1982, **LTR**; Evans, T. G. & Proctor, M. C. F., 5 October 1989; Rich, T. C. G., 30 June 2000 and three trees 2004, **NMW**.