

Viola rupestris and its hybrids in Britain

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ABSTRACT

Hybrids between *Viola riviniana* and *V. rupestris* were identified by means of isoenzymes from three of the four localities for *V. rupestris* known from Britain. Differentiating characters between *V. riviniana* and *V. rupestris* are primarily found in leaf shape and indumentum, flower colour, spur shape and capsule shape. The ecology of *V. rupestris* is presented and compared with that of the hybrid and *V. riviniana*.

KEYWORDS: *Viola riviniana* × *V. rupestris*, isoenzymes, morphology, distribution, ecology.

INTRODUCTION

In Britain *Viola rupestris* F. W. Schmidt has a very restricted distribution with four locality groups in northern England. Hybrids with *V. riviniana* (*V.* × *burnatii* Greml) have been recognized or suspected in those localities but the identification on morphological grounds has been regarded as provisional owing to lack of knowledge about variation in the parental species. Valentine (1975) still recognized the hybrid from only one of the *V. rupestris* localities, Widdybank Fell (Teesdale). The aim of this study is to identify British hybrids by means of isoenzymes and to discuss their morphology, ecology and distribution against that background.

V. rupestris has a wide palaeartic distribution, seemingly more-or-less continuous from eastern Siberia to northern and central Europe. To the west it reaches the Pyrenees, south-eastern France, western Germany and south-eastern Norway and has isolated locality groups on the Dutch dune coast and in northern England. Montane populations in northernmost Scandinavia are distinguished as subsp. *relicta* Jalas (Jalas 1950; Nordal & Jonsell 1998); otherwise no subspecies have been described.

V. rupestris has the chromosome number $2n = 20$, which is the lowest number known in the section *Viola*, but evidence from isoenzyme patterns has revealed that the basic number is $n = 5$ (Marcussen & Nordal 1998). *V. rupestris* belongs to the subsect. *Rostratae*, which in Britain is represented also by *V. persicifolia* Schreber ($2n = 20$), *V. reichenbachiana* Jord. ($2n = 20$), *V. canina* L. ($2n = 40$), *V. riviniana* Reichenb. ($2n = 37-46$, according to Valentine 1949) and *V. lactea* Smith ($2n = 58$). Crossing experiments between a number of these species were performed by Moore & Harvey (1961), who made conclusions about the distribution and sharing of genomes among them. *V. rupestris* was, however, not included in their study. For Britain Valentine (1975) reported only *V. riviniana* × *rupestris*, while previous records of the hybrid with

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V. canina were discarded as being based on *V. riviniana*. Outside Britain *V. rupestris* hybrids have been reported with *V. canina* and *V. riviniana* (and even with *V. hirta* L., which seems highly doubtful). For combinations with the two first-mentioned evidence at least from Scandinavia seems substantiated (Nordal & Jonsell 1998). The progeny of crossings undertaken between *V. canina* and *V. rupestris* and between *V. riviniana* and *V. rupestris* have shown pollen fertility between 0 and 5% and 0 and 14%, respectively (Bethke 1882; Erdner 1907; Becker 1910; Schöfer 1954; Schmidt 1961; Harvey 1966).

In a number of species of *Viola* sect. *Viola* it has been shown that isoenzymes vary little if at all within species and therefore can be used effectively as markers for the distinguishing of hybrids (Marcussen & Nordal 1997; Nordal & Jonsell 1998).

MATERIALS AND METHODS

All known *Viola rupestris* localities in England (Fig. 1) were visited by the authors from 8–12 May 1998 (Table 1, sites 1–4, 8, 12–13). Permission was granted by English Nature and landowners for very restrained collection of material. The intrapopulation homogeneity known from Nordic representatives of the sect. *Viola* (subsect. *Rostratae*, cf. Nordal & Jonsell 1998) justified restricted collection, an important consideration due to the relative rarity of the species. Analyses were undertaken on an average of about four (in practice 1–7) individuals per site. In most cases the sampling was non-destructive with removal of only a single leaf from the plant. A few whole specimens were transferred to a greenhouse at the University of Oslo for comparative cultivation. *V. riviniana* was sampled from the same or close sites (Table 1, sites 1–5, 8–13). In addition a particular search was made for putative hybrids.

The removed leaves were placed in plastic bags and kept cold with freezing elements for one week until they arrived at the laboratory. The transferred plants were immediately planted in pots and grown under greenhouse conditions with an 18 hour day at 16°C and a 6 hour night at 12°C.

TABLE 1. LOCALITIES AND ACCESSION NUMBERS OF SAMPLED POPULATIONS

Site	Grid reference	<i>V. rupestris</i>	hybrid	<i>V. riviniana</i>
Ingleborough				
1. Near Crummack Farm	SD/77.71	7650-2, 3 7651-2, 3, 4, 5		7652-1, 2, 3 7653-1
2. Long Scar	SD/76.72	7654-1, 2, 3, 4, 5		7655-1
3. Sulber Gate	SD/77.72	7656-3, 5		7656-2, 4, 6
4. Near Crummack Farm	SD/76.71	7659-1		7660-1, 2, 3
5. Near Crummack Farm	SD/77.71	7664-1, 2, 3		
6. Near Crummack Farm	SD/77.71		3771-1, 2, 3	
7. Long Scar	SD/76.71	3773-1, 2		
Teesdale				
8. Widdybank Fell	NY/81.29	7665-1, 2, 4, 7, 8 7666-1, 3, 4	7665-3 7667-1, 2, 3	7666-2
9. Widdybank Pasture	NY/84.30			7668-1, 2, 3
10. High Force	NY/88.28	7671-1, 2		7669-1, 2, 3
11. Cronkley Fell	NY/84.28			7674-1
Long Fell (Brough)				
12. Long Fell	NY/76.19	7678-6, 7, 8 7677-1, 2 7678-3, 4	7676-1, 3	7676-2
Arnside Knott				
13. Arnside Knott	SD/45.77	7679-1, 2, 3, 4		7680-1, 2

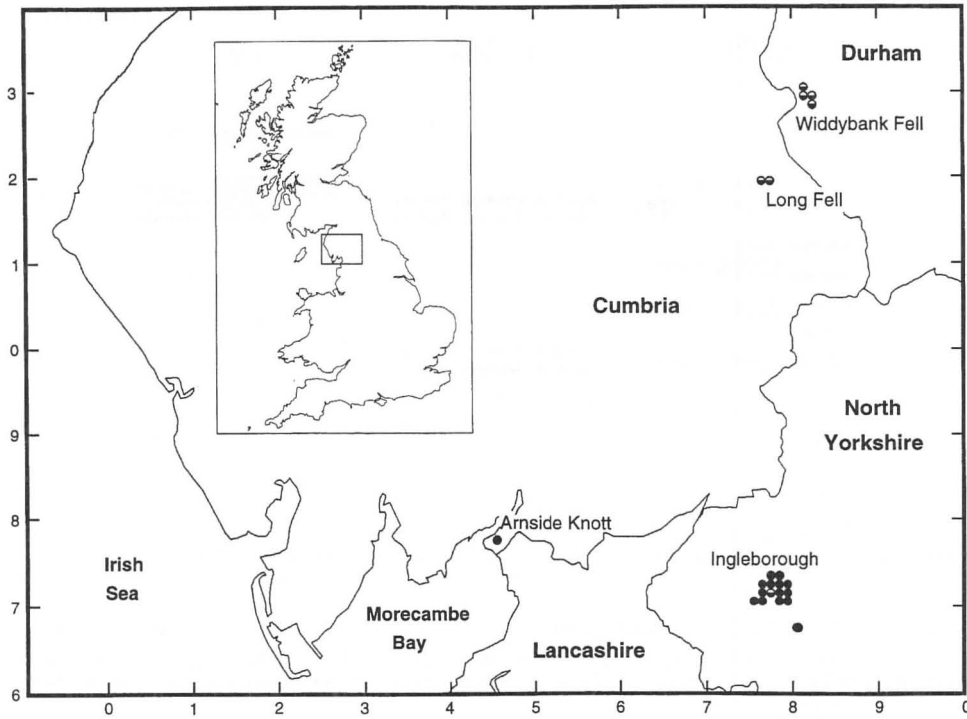


FIGURE 1. 1-km distribution of *Viola rupestris* (solid circles) and *V. rupestris* + *V. x burnatii* (half-circles) in Britain.

The field-sampled leaves and one from each of the transplanted specimens were crushed in a grinding buffer (Morden *et al.* 1987). The crude extracts were absorbed into paper wicks for subsequent horizontal starch gel electrophoresis (Wendel & Weeden 1990). Altogether, seven enzyme systems were analysed: IDH (isocitrate dehydrogenase), MDH (malate dehydrogenase), and PGM (phosphoglucumutase) were run on the so-called "D- system"; AAT (aspartate aminotransferase), AMP (aminopeptidase), GPI (gluco-6-phosphate isomerase), TPI (triose-phosphate isomerase) in the "A/B- system" (Selander & Yang 1969; Soltis *et al.* 1983, see also Nordal & Jonsell 1998).

After the plants had been in cultivation under similar conditions from May to October 1998 leaves from the (surviving) plants were pressed for comparison.

ISOENZYME RESULTS

Three of the isoenzymes revealed patterns that gave different band phenotypes in *Viola rupestris* and *V. riviniana* and an additive pattern in the hybrids: GPI, PGM and TPI (Fig. 2). The pattern was totally consistent so that hybrid constitution in one isoenzyme system always inferred hybrid constitution in the other two. The enzymes AAT, IDH and MDH did not differentiate between the two species, and accordingly cannot be used in hybrid analyses. The results for AMP indicate intraspecific variation in *V. rupestris*, which needs to be further elucidated.

The dimeric enzyme GPI showed activity in two regions (Fig. 2). In the anodal region two bands, always blurred, were displayed in both species and the putative hybrids. In the cathodal region a three-banded pattern was always found in *V. rupestris*, best interpreted as two allelic bands with an intermediate heterodimer, in a pattern of fixed heterozygosity, which may be expected in an allotetraploid. The octoploid *V. riviniana* always displayed a five-banded pattern, in

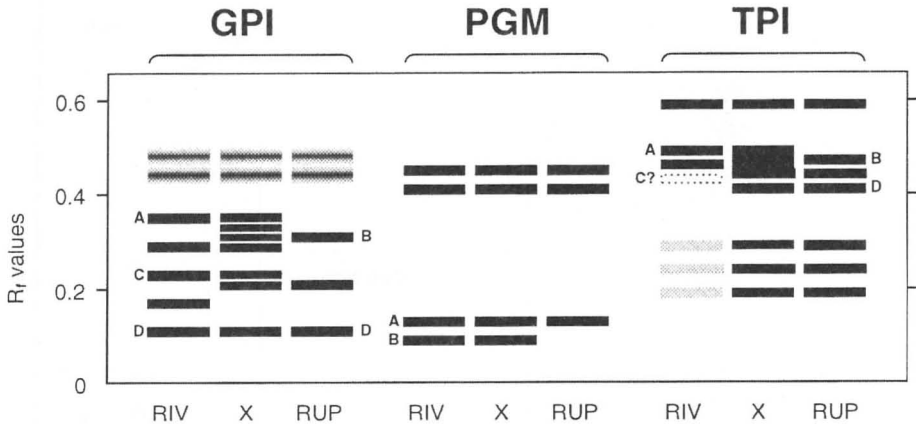


FIGURE 2. Isoenzyme results for gluco-6-phosphate isomerase (GPI), phosphoglucomutase (PGM) and triose-phosphate isomerase (TPI) for *Viola riviniana* (RIV), *V. × burnatii* (X) and *V. rupestris* (RUP).

which the second and the fourth bands probably constitute heterodimers. With this interpretation *V. rupestris* has the genotype BD and *V. riviniana* ACD in this complex "locus". The hybrids displayed an ABCD pattern with most of the constituent heterodimers, except the CD heterodimer, present in the individuals.

In PGM (a monomeric enzyme) activity was also revealed in two regions (Fig. 2). In the anodal area a fixed, identical two-banded pattern was shared by the two species. In the cathodal area *V. riviniana* most often showed two bands (A and B), whereas *V. rupestris* only revealed the B-band. In this case the hybrid pattern was identical with that of *V. riviniana*. In very few cases *V. riviniana* displayed a band in a more cathodal (C) position, and one hybrid (7665-3) displayed a triple-banded ABC pattern (not illustrated).

TPI (a dimeric enzyme) revealed a fairly complicated multibanded pattern, difficult to break down into allelic interpretation. The bands may be referred to three regions. The most anodal displayed one band shared by both species. Clear variation between the two species was found in the next region, where *V. riviniana* had activity in front of *V. rupestris* (Fig. 2) and where the hybrid revealed additivity. *V. riviniana* displayed two distinct bands in this region and *V. rupestris* three. The latter is best interpreted as a fixed heterozygote (BD) with an intermediate heterodimer. *V. riviniana* might have a third indistinct band and if so an AC-genotype, or the two distinct bands may represent two monomorphic loci which do not interact. These alternative interpretations will not influence the testing of the hybrid hypothesis. In the hybrids, with a putative AB(C)D constitution, the bands tend to fuse, as visualised in Fig. 2. In the third region both species showed a fixed three-banded pattern, – much weaker, however, in *V. riviniana* than in *V. rupestris* and the hybrid.

MORPHOLOGICAL OBSERVATIONS

SEPARATION OF *VIOLA RUPESTRIS* FROM *V. RIVINIANA*

Although a distinct species, *Viola rupestris* is sometimes difficult to distinguish from *V. riviniana*, especially when this species is represented by small-flowered forms (var. *minor* (Murbeck ex Gregory) Valent.) as is the case in most British localities where it grows with *V. rupestris*. The confusion is reinforced by the fact that *V. rupestris* is not consistently pubescent along petioles and peduncles and on capsules as is generally stated in current Floras (e.g. Stace 1997).

The most reliable separating characters for British plants of *V. rupestris* from *V. riviniana* are as follows:

1. Leaf shape: the laminas of *V. rupestris* are 'shovel-' or 'scoop'-shaped, with a clearly blunt apex, and with a less strongly cordate base than in *V. riviniana*. In *V. rupestris* the sides of mature leaves are often curled upwards (hence the 'scoop'), whereas in *V. riviniana* it is the basal lobes which are often upcurled. The areas of the lamina between the veins are somewhat raised in most forms of *V. riviniana*, giving a \pm dimpled effect to the blade; in *V. rupestris* the surface is flatter. The crenations at the leaf-edges are flat (i.e. within the plane of the leaf) in *V. rupestris*, but in *V. riviniana* are slightly 'crimped', and thus more obvious. In Fig. 3 leaf-silhouettes demonstrate, on limited material, clear differences particularly in the cordate shape of the blade, the rounded blade apex in *V. rupestris*, and the intermediate nature of the hybrid.
2. Indumentum: the highly distinctive fine, very short indumentum of *V. rupestris* usually extends up the peduncles, and up the petioles onto the margins of the basal lobes, leaving most of the upper lamina essentially glabrous in the great majority of plants. (In some variants, the fine indumentum extends all over the upper and lower surfaces of the lamina.) Where dense, the indumentum produces the impression of a grey 'fuzz' to the naked eye.

It should be noted that some *V. rupestris* individuals are glabrous even along petioles and peduncles. Such individuals were found, and confirmed by isoenzyme analysis, in all the localities except for Arnside Knott. Furthermore, plants may often be found with indumentum on some petioles but not on most.

The forms of *Viola riviniana* which accompany *V. rupestris*, while lacking this fine indumentum of dense short hairs, almost invariably carry on the upper lamina sparse long bristly hairs which are about 250–330 μm long, and thus typically about six to eight times longer than the indumentum 'hairs' of *V. rupestris*, which measure around 35–50 μm . These sparse, long, colourless hairs of *V. riviniana* can be inconspicuous, and are best observed by looking with a lens across the upper surface of a leaf bent over the finger to create a convex surface.

3. Flower colour: the corolla colour in *V. rupestris* is often paler and less blue than in *V. riviniana*, being a 'delicate pinkish-mauve' in Teesdale plants (M. E. Bradshaw, pers. comm.), although the colour may vary in both species, and also alters with exposure, bleaching and ageing processes. Looking into the flower from the front, in *Viola riviniana* there is usually a narrow band of darker violet separating the colour on the lower lip from the white in the throat; this band is apparently always lacking in *Viola rupestris*.

The flowers of the Arnside Knott colony, which have been sparsely produced in recent seasons, are always pure white, as first noted by Valentine & Harvey (1961). The plant is illustrated in Halliday (1997).

4. Spur: the spur of *Viola rupestris* is short, conical to a round tip without obvious groove or projection. The spur in *Viola riviniana* is long, stout, and often vertically grooved at the end, and often with a small projection from its upperside near the tip. (The colour of the spur varies in both species.)
5. Ripe capsule: the ripe capsule of *V. rupestris* is almost globular with truncate apex in side aspect, whereas that of *V. riviniana* is more elongated, and most often has an obtuse or even acute apex.
6. *V. rupestris* produces rosettes on lateral branches, which are often hidden within the substrate. Such branches are non-rooting, so that the rosettes do not become independent plants, although often giving this appearance (Bradshaw & Doody 1978b). *V. riviniana*, however, has genuine vegetative propagation in that adventitious shoots (sobelos) may develop on the root system (Valentine 1949).

It is worth noting that the forms of *V. riviniana* which occur in exposed sites close to *V. rupestris* can approach that species. In comparison with *V. riviniana* forms in nearby, more sheltered, sites such as block scree and fissures in limestone pavement they have a deeper green colour overall, are more prone to developing purple tints, have a much more condensed form with short petioles producing a tight rosette, have more leathery leaf texture, and smaller flowers.

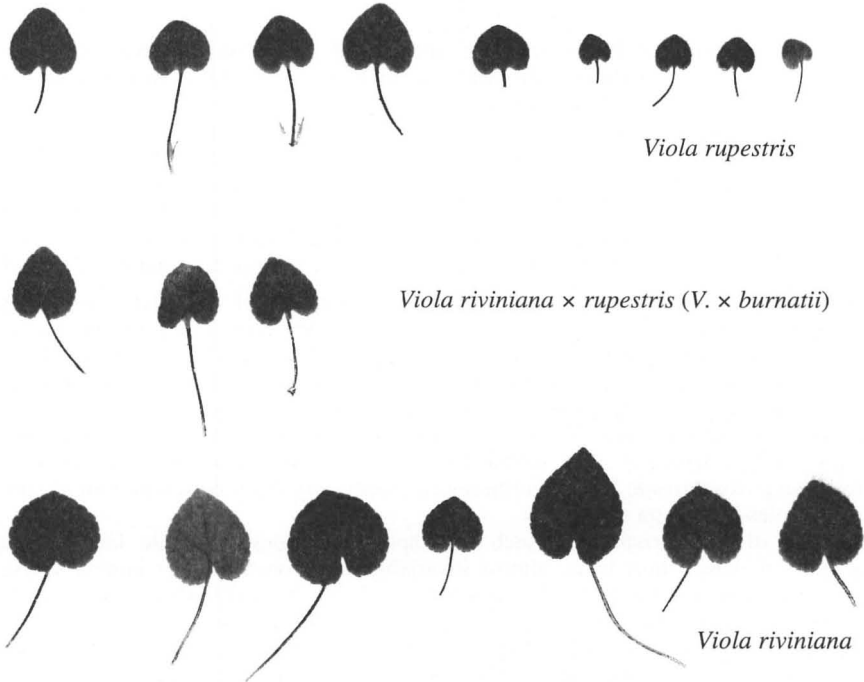


FIGURE 3. Leaf silhouettes of *Viola rupestris*, *V. x burnatii* and *V. riviniana*. Scale c. $\times 0.6$.

HYBRID MORPHOLOGY

Detection of the generally rare hybrids in the often abundant and dense populations of the species is not straightforward, due to variation of the parent species in all of the above characters, and the low stature of the plants.

In plants examined to date, hybrids may be suspected by an intermediate leaf-shape (Fig. 3) and by the presence **both** of the dense short indumentum of *V. rupestris* - albeit patchy - on petioles and stems, **and** of the sparse longer hairs of *V. riviniana* on the upper leaf lamina. Some hybrid plants can appear glabrous, as with a proportion of the *V. rupestris* parent; however, a few hairs, sometimes of intermediate length and form, will generally be found on upper laminas, particularly on the midrib or patchily towards the basal lobes. Where the indumentum is well-developed, it is most abundant on the upper part of peduncles, but is less reliably found on petioles.

Chasmogamous (i.e. opening) flowers appear to be produced less frequently in most seasons than by the parents. In colour and shape they tend to bridge the rather narrow differences between the parents. Flower shape tends to approach *V. rupestris* rather than *V. riviniana*. The dark bar in the throat usually characteristic of *V. riviniana* is in the hybrid faint or more-or-less absent. The dark purple colour of the veins (honey-guides) varies in density, and where they run out onto the mauve of the lower petal the pigmentation becomes more diffuse, contributing to the effect of a bar.

Aborted flowers and lack of fruits late in the season (when cleistogamous flowers have been produced) strongly indicate hybrid plants. The hybrid is thought never to ripen capsules, so that the presence of ripe capsules in late summer, often abundant on mature plants, reliably indicates the species. Hybrids can most easily be detected at this time when the plants attain their greatest stature and leafiness.

The soboles of *V. riviniana* are apparently inherited by at least some hybrid plants, allowing indefinite survival of individual plants. In the Long Fell (Brough) and Widdybank Fell (Teesdale) localities, hybrid patches of considerable size (and perhaps age) are known, up to 1-2 metres in diameter or more, and giving the appearance of clonal derivation from rare hybridisation events.

The production of adventitious shoots is particularly vigorous in the hybrid; on Widdybank Fell densities of rosettes were recorded on trial plots of 656/m² for the hybrid, 149/m² for *V. rupestris*, and 175/m² for *V. riviniana* (Bradshaw & Doody 1978a).

ECOLOGICAL OBSERVATIONS

HABITATS OF *VIOLA RUPESTRIS*

In all its four English locations, *Viola rupestris* grows on exposures of Carboniferous limestone. *V. rupestris* tends to occur in the more open and more exposed habitats available, on the thinnest soils. It has two typical favoured habitats: one is on the eroding tops and flanks of low limestone hummocks growing either in fine cracks in the bedrock, or in a 'clitter' of small stones lying over the bedrock or as gently sloping scree; the other is in fine scree (more-or-less consolidated) below low escarpments. It also occurs much more sparsely on the 'clints' (or flat tops) of limestone pavements, but only where the rock surfaces are sufficiently fissured or the rock is covered in 'clitter' - the loose stones resulting from degradation and fracture of the bedrock.

On the sites south-east of Ingleborough, some of the largest colonies are also on gently- to steeply-sloping faces of drift deposits over limestone. Bare clayey soil, evidently calcareous, is a feature of this habitat, the open nature of the sites apparently being maintained over long periods by soil-creep and by stock trampling. The colonies lie between 320–425 m a.s.l.

On Widdybank Fell the plant occupies exposures of granular partially-metamorphosed limestone ('sugar limestone'), the rapid erosion of which creates zones of loose calcareous rubble and coarse calcite 'sand'. *Viola rupestris* appears to be an early colonist of such bare soils, with little else besides a thin turf or occasional tufts of *Festuca ovina* L. and plants of *Minuartia verna* (L.) Hiern. The species persists in closed *Festuca* turf, although flowering and fruiting less vigorously, and only where some disturbance (such as by moles) maintains areas of open soil. The development of denser closed swards appears eventually to oust the violet. Plants occur from 490–510 m a.s.l.

The Long Fell colonies lie at 575–610 m a.s.l. on a shelving S.S.W.-S.E.- facing escarpment, the plants growing on slopes above cliffs, with a few patches on narrower ledges below the uppermost low cliffs of the scarp. Eighteen colonies were located in 1998. The plants are consistently dwarf in comparison with those at the other three sites; it is unclear whether this dwarfing is a response to the greater exposure and altitude (Heaton 1999). The dwarf form appears to be retained in cultivation.

Its most typical closest associates in the upland sites, whether on un-metamorphosed limestones or calcareous boulder clay, are *Carex flacca* Schreber, *C. panicea* L., *Carlina vulgaris* L., *Euphrasia confusa* Pugsley, *Sesleria caerulea* (L.) Ard., and *Thymus polytrichus* Borbás. It can be found in open turf of *Festuca ovina* and *Sesleria caerulea*, but rarely in dense turf of either species.

At Arnside Knott there exists the only colony of *Viola rupestris* known off the 'high' limestone. This site is on an exposed escarpment, in a very limited area free of scrub at 150 m a.s.l. (Lists of associates in the Arnside, Long Fell, and Widdybank localities are given in Valentine & Harvey 1961).

HABITATS OF *VIOLA RIVINIANA*

Viola riviniana almost invariably occurs in the near vicinity at all four sites, but is seldom intermingled. It obviously survives in closed turf of *Festuca ovina*, where *V. rupestris* is rare or absent, but conversely it avoids open 'clitter' areas of small stones or fine scree, colonised by *V. rupestris*. In a very dwarf and condensed form it is widely present also in the closed *Agrostis*/*Festuca* grasslands between the limestone outcroppings. As a much larger and laxer plant with large flowers it occurs, often abundantly, in the hollows between larger stones and in the 'grykes' (vertical fissures) of limestone pavement.

HABITATS OF HYBRIDS

The hybrid prefers deeper soils, and can tolerate denser turf, than *V. rupestris*, but has not yet been seen far from colonies of the rarer parent. On Widdybank Fell the habitat consists of semi-open or closed swards generally intermediate between those preferred by the parents. It also occurs with

Calluna on calcareous brown-earth soils, where moles are active (Bradshaw & Doody 1978b). On Long Fell one patch of hybrid plants was on a gently-sloping south-facing patch of loose stones immersed in black humus-rich soil, over bedrock. The few plants on Ingleborough have been found in open patches on drift covered in loose stones, between areas of *Festuca ovina* turf, within a few centimetres of the parent species.

POPULATION SIZES OF *VIOLA RUPESTRIS* AND THE HYBRID

Viola rupestris occurs most typically in local, dense colonies of a few to very many rosettes within limited tracts of its preferred habitat, whereas *V. riviniana* occurs more dispersed, but over much more extensive turf habitats between outcroppings of limestone. Work on establishing the population sizes and spatial limits of *V. rupestris* is continuing. As previously remarked, due to the difficulty of establishing the origin of rosettes, it has been usual to regard each rosette as an individual for recording purposes. Surveys in 1998 on parts of the known distribution on the south-east spurs of Ingleborough suggest that the population of the whole will amount to tens or hundreds of thousands of individuals. The Widdybank sites are estimated to have thousands of individuals (M. E. Bradshaw, pers. comm.), whilst the population on Long Fell was estimated in 1998 at between 1000 and 2000 plants. Arnside Knott had 56 plants in 1998 (Heaton 1999).

Hybrid numbers in 'the high hundreds' are known on Widdybank Fell, with ten dense colonies and scattered groups and singles (M. E. Bradshaw, pers. comm.). It appears to be more localised on Long Fell, although this area has been worked much less thoroughly than has Widdybank Fell; the patches known in 1998 had a few dozen rosettes. On the Moughton/Crummack/Norber sites south-east of Ingleborough, however, only a few individual hybrid plants have yet been located in over 50 colonies of *V. rupestris* examined.

DISCUSSION

In the presented isoenzyme patterns of GPI and TPI, *Viola rupestris* in England displays exactly the same band patterns as were found in Nordic populations of the same species (Nordal & Jonsell 1998). The A-band in PGM in the English plants is shared with plants belonging to the North Scandinavian *V. rupestris* subsp. *relicta* and is different from the widespread ssp. *rupestris*. This indicates an interesting connection which will be analysed in a wider geographical context (Jonsell & Nordal in prep.). The *V. riviniana* plants analysed from the English localities have different band patterns compared to Nordic material in all the isoenzymes presented. Our English *V. riviniana* material consistently showing this isoenzyme pattern includes both small-flowered forms which often grow together with *V. rupestris* and larger-flowered ones from sites in the vicinity.

Based on enzymatic evidence hybridisation was revealed in all but one of the four British areas for *V. rupestris*. The exception is Arnside Knott though *V. riviniana* is frequent both on and close to the spot. In two of them (Widdybank Fell and Long Fell) the hybrid was previously known, while the record from Crummockdale (Ingleborough) is new (for details see Table 1). Of five sites for *V. rupestris* sampled in the Ingleborough area, where *V. riviniana* is common throughout, the hybrid was revealed only in one. This suggests that hybridization is comparatively rare there, although one has to allow for the difficulties of distinguishing hybrids in the field. The hybrids analysed give the impression of being F1 individuals and we have seen no traces of back-crossing to parents. This is in contrast to the situation in parts of Scandinavia where, according to preliminary observations (Nordal & Jonsell 1998), there are trends towards genetic swamping of *V. rupestris*, where this species is rare. There, however, *V. canina* seems usually to be the other parental species, though hybridisation with *V. riviniana* has also been documented (Nordal & Jonsell 1998).

In many seasons *V. rupestris* is sparsely-flowered - at least as regards chasmogamous flowers, which appear mainly during May. Thus, given the very exposed habitats in which it typically grows, with little insect activity in the early season, the chances of cross-pollination of its chasmogamous flowers with those of *V. riviniana* are clearly low. These factors may account for the observed rarity of hybrids in most sites. Although both species appear to regenerate efficiently from seed the vast majority of seeds are likely to result from selfing within cleistogamous flowers.

Whilst the fell-field habitats are undoubtedly over-grazed by sheep at present, the resultant erosion helps to retain open unstable areas suitable for colonisation of *V. rupestris*, but less favourable for propagation of hybrid clones, which need more stable substrates. The sterility of any hybrids, and consequent apparent lack of back-crossing, coupled with the abundant seed-production of the pure species, dictate against any swamping of *Viola rupestris* populations in the foreseeable future.

The close spatial juxtaposition of the habitats of the two species means that they may be found in close proximity. The apparent tolerance of *V. rupestris* for eroding habitats with their mineral soils, where it evades competition not only from *V. riviniana* but also the turf-forming grasses, appears to have allowed its local survival. An observation by F.J.R. requiring further investigation is that in other areas of the north of England where Carboniferous limestone is exposed in apparently similar situations and climate, *V. riviniana* appears to occupy the types of microhabitat preferred by *V. rupestris* in its few stations.

ACKNOWLEDGMENTS

We would like to thank the following for help in various ways: Dr M. E. Bradshaw, Erica Donnison (English Nature, Cumbria Team), Peter Corkhill (Ingleborough National Nature Reserve), Kristian Heaton (Edge Hill University College), Stephen Hewitt (Tullie House Museum, Carlisle), John Hooson (National Trust), Chris McCarty (Teesdale National Nature Reserve), Major Ken Miles (Range Officer, M.O.D. Warcop Training Range), and Jacqui Ogden (English Nature, Cumbria Team). The distribution map in Fig. 1 was prepared using DMAP software produced by Dr Alan Morton.

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(Accepted March 2000)