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Variation in Viola rupestris Schmidt

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During the IPE, collections of *V. rupestris* were made in four localities, as follows:

Radvaň, near Bánská Bystrica, Slovakia, July 5th.
Zadielský Kámen, Slovakian Karst, July 7th.
Sivá Brada, Slovakia, July 10th.
Pálavské vrchy (Pollauer Berge), Moravia, July 23rd.

V. rupestris is a diploid species ($2n = 20$) with a geographical distribution which extends from Great Britain in the West to the Pacific coast of the Soviet Union in the East; it is included by Hultén (1950) in his group of West-Sibirian continental plants. In Europe, it is commonly a species of soils of light texture (loams or sands) and is often found on soils rich in bases. In addition, it is also generally a species of open habitats, and it does not occur in dense shade or where the community is completely closed. The habitats listed above are typical in all these respects. It was not possible to make full descriptions of the communities, but the following data (Table 1) were obtained.

Examination of the herbarium specimens showed marked differences between the four collections in size, habit and indumentum; some of these differences are noted in Table 2. In order to test whether the differences were due solely to the direct effect of the environment on the phenotype, or had a genetic component as well, seeds which had been collected in the field from three of the populations were sown in the autumn of 1958; (unfortunately, it was not possible to collect seed from population No. 2 on the Slovakian Karst). The seeds sown all germinated well in the spring of 1959 (germination varied from 40 to 100%), and families of seedlings were planted out in boxes where they made vigorous growth. The soil used was a John Innes compost made up of sterilised loam, peat and sand to which artificial fertilisers (N, P, K, Ca) had been added. Representative plants, photographed in September after 5 months' growth, are shown in Fig. 1; each of the families was very uniform and showed little variation. In the spring of 1960, plants of all three populations produced flowers, and no differences in floral characters could be detected. All the flowers were of the normal pale violet colour and of approximately the same size. Data on other characters are summarised in Table 3.

Table 1

1	*2*	*3*	*4*
Radvan, dolomite	*Zadielsky Kámen*, dolomite	*Sivá Brada*, travertine	*Pálavské vrchy*, limestone
Open rocky ground, ca. 550 metres	Very open rocky ground, slight slope facing south, ca. 600 metres	Open rocky ground, open grassland, ca. 500 metres	Very open slopes, facing S. or S. W., ca. 400 metres
V. rupestris scattered in crevices of rocks,	*V. rupestris* scattered in crevices of rocks,	*V. rupestris* in cracks of dry travertine and sparsely in surrounding grassland,	*V. rupestris* locally frequent in crevices in bare rock,
Also:	Also:	Also:	Also:
Fagus silvatica *Juniperus communis* *Pinus silvestris* as shrubs or small trees, scattered	*Crataegus monogyna* (1 m.) *Prunus mahaleb* (15 cm.)		
Arenaria serpyllifolia *Helianthemum chamaecistus* *Inula ensifolia* *Potentilla heptaphylla* *Poterium sanguisorba* *Sedum sexangulare* *Sempervivum hirtum* *Seseli osseum* *Thymus praecox*	*Achillea nobilis* *Echium vulgare* *Euphorbia cyparissias* *Minuartia setacea* *Potentilla arenaria* *Potentilla argentea* *Seseli glaucum* *Teucrium montanum*	*Allium montanum* *Asperula cynanchica* *Dianthus carthusianorum* *Galium verum* *Helianthemum rupifragum* *Hippocrepis comosa* *Lotus corniculatus* *Plantago media* *Potentilla arenaria* *Ranunculus acer* *Sempervivum hirtum* *Thymus* sp.	*Asperula glauca* *Minuartia setacea* *Potentilla arenaria* *Poterium sanguisorba* *Scabiosa ochroleuca* *Teucrium montanum* *Thymus* sp.
Anthericum ramosum *Festuca duriuscula*	*Agrostis alba* *Carex humilis* *Festuca duriuscula* *Poa badensis*	*Carex humilis* *Festuca pseudo-ovina*	*Andropogon ischaemum* *Festuca duriuscula* *Poa badensis*
	Asplenium ruta-muraria	*Grimmia apocarpa* *Tortella tortuosa*	

Table 2. Data from herbarium specimens

	(1) Radvaň	(2) Zadielský Kámen	(3) Sivá Brada	(4) Pálavské vrchy
Indumentum	Whole plant hairy	Whole plant glabrous	Some plants with glabrous capsules, some with glabrescent capsules. All other parts of all plants, including sepals, hairy.	Whole plant hairy
Mean stem length cm.	3	4	7	2

Fig. 1. Plants of *Viola rupestris* of the same age, grown from seed under uniform conditions at Durham.
Seed from: A. Radvaň; B. Sivá Brada; C. Pálavské vrchy.

Table 3. Data from families of living plants, grown under uniform conditions, from seed collected in the field

	(1) Radvaň (12 plants)	(3) Sivá Brada (12 plants)	(4) Pálavské vrchy (20 plants)
Indumentum	All plants of parental type i.e. all hairy	Capsules of 2 plants glabrescent, remaining plants with glabrous capsules. Plants otherwise hairy	All plants of parental type i. e. all hairy
Mean stem length (cm.) and Standard error	17 ± 1 · 1	6 · 5 ± 0 · 36	14 · 5 ± 1 · 08
Mean leaf length (mm.) and Standard error	29 ± 1 · 2	21 ± 0 · 61	24 ± 0 · 84
Mean seed weight (mg.)	1 · 06	0 · 58	1 · 07
Anthocyanin	Stems red	None	Stems, petioles, leaves coloured red
Chromosome number, 2n	20	20 ± 1	20

The most striking result here is the difference between family No. 3 (Sivá Brada) and the other two families. It differs significantly from the other two in stem length, seed weight, anthocyanin colouration and indumentum. The most interesting of these characters is that of size. It would appear that the moderately small parent plants from Sivá Brada (Table 2, stem length 7 cm.) have produced offspring of about the same height (Table 3, stem length 6 · 5 cm.), while the very small parent plants from localities 1 and 4 (Table 2, stem lengths 3 and 2 cm.) have produced large offspring (Table 3, stem lengths 17 and 14 · 5 cm.). We may elucidate this result in the following way. In none of the natural habitats are the plants very large; this comparatively small size in nature may possibly be regarded as adaptive. If this be assumed, then it would appear that in one of these populations (Sivá Brada), the adaptation has become genetically fixed, while in the other two it has not; in the latter, although the phenotype is small, the plants are still capable, under the favourable environmental conditions of the experimental garden, of growing to a relatively large size. The variation in the constitution and behaviour of topodemes is not uncommon; it was commented upon by TURESSON (1922) in one of his early papers on genecology. (The use of the word topodeme, to describe a population from a particular locality, is described in a paper by GILMOUR and HESLOP HARRISON (1954).

Discussion

This investigation forms part of a larger project for the exploration of the range and nature of variation in *V. rupestris*. It is clear from the literature that *V. rupestris* is a variable species; in particular, authors of floras have drawn attention to variation in flower colour (such as is found in many other species of the genus *Viola)* and to variation in degree of hairiness. A complete range of forms from practically glabrous (var. *glaberrima* Murb.) to very hairy (var. *arenaria* DC.) is known. The suspicion that variation in this character often has a genotypic basis is confirmed by our experiments in which, in each case, the offspring have bred true for the parental indumentum characters. The particular combination of characters shown by the Sivá Brada plants, viz. capsule glabrous or glabrescent, rest of plant hairy, is, so far as we know, not described in the literature, though it is paralleled in the allied American species *Viola adunca* Sm., discussed below.

As Table 3 shows, the variation described here is concerned not only with hairiness, but with a number of other characters such as size, seed weight, distribution of anthocyanin etc. What is not clear is to what extent this type of variation is correlated with habitat or with geographical distribution. Can, for example, the differences between the populations on dolomite and travertine be paralleled in other parts of Central Europe? Do populations from sandy soils such as are known both in Czechoslovakia and Poland differ consistently from those on calcareous rocks?

Preliminary attempts to answer these questions by examination of herbarium material have been made, but with no success. The plant in the field is often dwarfed and poorly developed, the collections are often scrappy, and ecological data on the herbarium sheets are generally lacking or inadequate. It is only by making special collections and observations, such as are reported here, that the answers to such questions can be found; and this is one of the reasons why occasions such as the IPE are so valuable.

We have suggested that the kind of variation described may be explained in terms of adaptation to differences in habitat or climate. Another kind of explanation is possible, which depends upon the breeding system of the plant. In all violets of the section Nomimium, cleistogamous as well as open flowers are produced. The latter are visited by insects and may be cross-pollinated; the former never open and are always self-pollinated. The proportion of seed produced by the two types of flower in wild populations of *V. rupestris* is not known and has probably never been observed. However, observations on British populations of the allied species *V. riviniana* (VALENTINE, 1941) showed that, in one season, 19 plants in the field produced 35 capsules from open flowers and 63 capsules from cleistogamous flowers; and it would seem that the proportion of selfed capsules of the latter type is generally high in this group of violets. This means that in any population there will be a good deal of inbreeding; and this will be accentuated in *V. rupestris,* where the populations often seem to be local and discontinuous. The effect of this breeding system, i. e. occasional out-breeding and frequent inbreeding, will be to produce local populations genotypically more or less uniform or consisting of only a few biotypes, which will probably differ slightly and genotypically from neighbouring populations. This is the situation actually found in *V. riviniana* in Britain (VALENTINE, 1941), and a similar population structure in *Viola rupestris* is to be expected. It is perhaps worth noting that preliminary studies on *Viola adunca* Sm., a widely distributed North American species, allied to *V. rupestris,* indicate that this species too has this kind of population structure.

There is yet another possible cause of variation, and that is interspecific hybridization. Natural hybrids between *V. rupestris* and *V. riviniana* Rchb. and *V. reichenbachiana* Jord., are recorded in the taxonomic literature (BECKER, 1910) and have also been described by VALENTINE (1950) and SCHÖFER (1954). These hybrids have always been found to be highly infertile, with chromosomal irregularities at meiosis; but the occurrence of putative hybrids with a series of chromosome numbers from $2n = 20$ to $2n = 44$ (as demonstrated by SCHÖFER) indicates that some hybrids may possibly reproduce and give rise to selfed or back-cross generations which may in time establish new populations. The fact that all the populations described above are fully self-fertile and diploid, and that no other violet of the Rostratae group (such as *V. riviniana)* was found growing with them, makes the hypothesis of hybridization unlikely in this particular case; but it has to be borne in mind as a possibility.

These considerations clearly have a bearing on the systematics of *V. rupestris.* It may well be possible to describe very many slightly different forms of the species, but there would seem to be no point in doing so. Thus, hairiness is a character which appears to vary somewhat at random in the species, so that it does not seem justifiable at present to give a higher rank than «forma» to the hairy, glabrescent and glabrous groups. Whether there are any broad ecological or geographical groupings to be made in this species remains to be seen. It is perhaps worth drawing attention here to the work of Australian botanists on the inbreeding species *Trifolium subterraneum* L., which has been widely introduced into Australia, where it is a pasture plant of great economic importance. Detailed studies (MORLEY and FRANKEL, 1959) have shown not only that the species is very variable, but also that variation in physiological characters, such as vernalization requirement and time of flowering, is widespread and tends to show a regional distribution. It is possible that some of the variable and apparently non-adaptive characters of *V. rupestris* may be «indicators» of important physiological differences concerned with habitat or climatic tolerance. If progress in this direction is to be made, more collections both of herbarium material and of seed are needed, first from different habitat types in Europe, but more particularly from the eastern parts of the geographical range. We have not yet examined any Russian herbarium material; but it is perhaps worth quoting the statement of JUZEPTCHUK (1949) in the Flora of the USSR: «... a detailed study of the racial composition of *V. rupestris* s. l. over the whole extent of its very large area is needed.» This paper represents merely a preliminary step towards the solution of the wider problem.

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