

Frequencies of pin and thrum plants in a wild population of the Cowslip, *Primula veris* L.

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ABSTRACT

The heterostylous dimorphism in the genus *Primula* is discussed. A population of the cowslip *Primula veris* on stable duneland at Strathy in Sutherland contained an excess of the thrum form. It is suggested that this may be due to an advantage of the heterozygous thrums over pins in some microclimates.

The heterostylous dimorphism in the genus *Primula* is well known. Two types of flower exist, always borne on separate plants. In the 'pin' form, the anthers are placed half-way down the corolla-tube, the mouth of which is occupied by the stigma, borne on the end of a long style. In the 'thrum' flowers, the positions of the sexual organs are reversed, the anthers being at the top of the corolla-tube while the stigma is half-way down it, since the style is relatively short.

Darwin (1877) recognised that this dimorphism mechanically favours outbreeding since insects tend to transfer pollen to stigmas at the same level as the stamens. Yet more important in achieving outbreeding in this genus are the physiological distinctions between the pin and thrum forms, which result in pollen being largely incompatible on its own kind of stigma. The basis of this incompatibility is differential pollen-tube growth (Tseng 1937, Lewis 1942).

Pollen from thrum anthers can germinate on a thrum stigma but rarely penetrates its surface, so that fertilisation is not achieved. As Ford (1964) has pointed out, this incompatibility occurs whether the pollen is genetically pin or thrum and is an example of Mendelian inheritance delayed one generation. Pin pollen readily germinates on and penetrates the surface of a pin stigma, but pollen-tube growth is then slow compared with that of the thrum form, which in these circumstances will always reach the ovules first. Thus of the two 'illegitimate' crosses, thrum \times thrum probably never succeeds in wild populations while pin \times pin regularly does so, but only in the absence of thrum pollen.

The genetic control of the pin/thrum heterostyly in *Primula* is by means of a supergene the components of which control both physiological and structural characteristics of pin and thrum flowers (Ernst 1928). The various loci comprising this supergene are closely linked and normally behave as if they were a pair of alleles (*S* and *s*), with the thrum character dominant to pin (Bateson & Gregory 1905).

As a result of the incompatibility mechanisms mentioned above, thrum homozygotes probably never occur and pin selfing is restricted to special circumstances (where thrum plants are absent). Thus the breeding system gives rise to a series of backcrosses (*Ss* \times *ss*) with pin and thrum seed being produced in approximate equality. In wild populations of *Primula vulgaris* Huds., the species most studied in the genus, equality of pin and thrum plants is seldom found and a slight excess of pin is the norm, probably owing to its capacity for self-fertilisa-

tion (Crosby 1949, Ford 1964). Excesses of thrums have however also been found (Haldane 1938).

The report presented here concerns a large population of the cowslip, *Primula veris* L., from stable duneland at Strathy in Sutherland. Four samples of plants were collected along a transect running down the SW. side of a SE./NW. cleft in the dunes. Its length was about 70 yards, dropping 60 feet from the top sample A to the bottom sample D. Care was taken to collect only one flower per plant. Details of the results are given in Table 1.

TABLE 1. DETAILS OF SAMPLING AREAS AND OF SAMPLES OF *PRIMULA VERIS* OBTAINED FROM STRATHY, SUTHERLAND

Site	Approx. slope of dunes	Associated plant species	Pin	Thrum	Total	% Thrum
A	20°	<i>Agropyron junceiforme</i> (A. & D. Löve) A. & D. Löve <i>Bellis perennis</i> L. <i>Festuca rubra</i> L. <i>Plantago lanceolata</i> L. <i>Thalictrum minus</i> L. <i>Ditrichum flexicaule</i> (Schwaegr.) Hampe	60	93	153	60.8
B	30°	<i>Agropyron junceiforme</i> (A. & D. Löve) A. & D. Löve <i>Bellis perennis</i> L. <i>Festuca rubra</i> L. <i>Galium verum</i> L. <i>Heracleum sphondylium</i> L.	67	71	138	51.4
C	40°	<i>Plantago lanceolata</i> L. <i>Vicia sepium</i> L. <i>Hylocomium splendens</i> (Hedw.) B., S. & G. <i>Pseudoscleropodium purum</i> (Hedw.) Fleisch. <i>Rhytidadelphus squarrosus</i> (Hedw.) Warnst.	44	75	119	63.0
D	<5°	<i>Achillea millefolium</i> L. <i>Agropyron junceiforme</i> (A. & D. Löve) A. & D. Löve <i>Agrostis stolonifera</i> L. <i>Centaurea nigra</i> L. <i>Festuca rubra</i> L. <i>Heracleum sphondylium</i> L. <i>Plantago lanceolata</i> L. <i>Sanguisorba officinalis</i> L. <i>Tussilago farfara</i> L. <i>Vicia sepium</i> L. <i>Equisetum arvense</i> L. <i>Hylocomium splendens</i> (Hedw.) B., S. & G.	80	81	161	50.3

The samples are homogeneous ($\chi^2_{(3)} = 7.04$, $P > 0.05$) and show a significant departure from the expected equality of pin and thrum, there being an excess of thrum in all of them ($\chi^2_{(1)} = 8.32$, $P < 0.01$). Style-length in the pin flowers was variable throughout and in some the style was so short that these were initially scored as short homostyles.

A wild sample of 522 *Primula veris* plants collected by Darwin (1877) contained 281 thrums and 241 pins, but he does not mention the locality where they were found. It is possible that the excess of thrums in this population and in that at Strathy is due to an advantage of the heterozygous thrums over pins. The relatively large excess of thrums in areas A and C at Strathy could reflect an increased advantage of the heterozygotes in the microclimates of these areas; both areas A and C had a sparse cover of vegetation whereas B and D had a thicker cover. Fixed dunes in general tend to have an extreme and locally very variable climate (Salisbury 1952). In a quite different organism, the polymorphic land snail *Cepaea nemoralis* L., rapid changes in the frequency of colour morphs over short distances have been recorded on duneland (Cain 1968). This has been related to its complex topography, producing microclimates (e.g. cold hollows) within which some morphs are better able to survive than others.

An attempt will be made to sample cowslip populations from as many areas of Great Britain as possible to establish whether an excess of thrum plants is normal in wild populations. Such a survey might also show if wild homostyle colonies exist in the cowslip, as in the primrose.

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