Studies on *Cytisus scoparius* (L.) Link with particular reference to the prostrate forms

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ABSTRACT

The distribution in the British Isles of the prostrate forms of *Cytisus scoparius* (L.) Link is given. Cultivation experiments show that growth habit is genetically determined. Whereas in wild populations the prostrate form at Dungeness is indistinguishable in growth habit from subsp. *maritimus* (Rouy) Heywood, there are significant differences under cultivation, when the Dungeness plants show a growth habit intermediate between subsp. *scoparius* and subsp. *maritimus*. Preliminary results from transplant experiments are reported.

Hybridization has been effected between erect and prostrate forms. Results suggest a difference in expression of the genes controlling growth habit in the wild and horticultural varieties of subsp. *scoparius*. The chromosome number of *Cytisus scoparius*, erect or prostrate, is $2n = 46$, although isolated counts of $2n = 48$ may be found.

INTRODUCTION

Cytisus scoparius (L.) Link (*Sarothamnus scoparius* (L.) Wimmer) is a common species throughout Western Europe. It is very variable in height and Böcher & Larsen (1958) have described a number of races or ecotypes which are primarily recognisable on this character.

The extreme prostrate form of the taxon, recognised as *Cytisus scoparius* (L.) Link subsp. *maritimus* (Rouy) Heywood, is genetically distinct from the erect subsp. *scoparius*. This was shown by Tutin (1953) and Böcher & Larsen (1958), who demonstrated that subsp. *maritimus* maintains its prostrate habit in cultivation. According to Tutin, subsp. *maritimus* is the same as *Sarothamnus scoparius* subsp. *prostratus* (Bailey) Tutin.

Many reports of the chromosome number of *Cytisus scoparius* subsp. *scoparius* are available but no general agreement on one particular number has been reached. Most early authors gave a count of $2n = 48$ (Kawakami 1930; Sugiura 1931, 1936; Tscheckow 1931; Kihara, Yamamoto & Hosono 1931; De Castro 1949; Morton 1955; Böcher & Larsen 1955). Maude (1940) reported a count of $2n = 46$. This count of $2n = 46$ has been confirmed by Böcher & Larsen (1958), Melecka (in Skalinska *et alia* 1964) and Gilot (1965). In their 1958 paper, Böcher & Larsen stated that their previous count of $2n = 48$ (1955) arose from the misinterpretation of two large satellites as a separate pair of chromosomes. The chromosome number of subsp. *maritimus* has been recorded as $2n = 24$ (Morton 1955), $2n = 48$ (Adams 1957) and $2n = 46$ (Böcher & Larsen 1958).

From 1957 to 1961 a study of *Cytisus scoparius* formed part of a larger programme of experimental taxonomic and genetical investigation undertaken at Liverpool. This work was supported by a D.S.I.R. grant made to one of us

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(S.W.). The work on *Cytisus scoparius* is a long-term project but the results so far obtained are presented here.

The distribution of the prostrate forms in the British Isles has been ascertained and studies have been carried out on both wild and cultivated populations, with particular reference to their growth habit, cytology and hybridization.

DISTRIBUTION AND HABITAT OF THE PROSTRATE FORMS IN THE BRITISH ISLES

Subsp. *maritimus* occurs in various exposed cliff habitats in the British Isles and populations in Caernarvonshire, Pembrokeshire, Devon (Lundy Isle), Cornwall, Co. Cork, Co. Kerry (Valencia Isle) and the Channel Isles have been reported (Scully 1916, Wright 1933, Rees 1942, Tutin 1953, Morton 1955, Adams 1957, Böcher & Larsen 1958). A prostrate population has also been noted at Dungeness in Kent (Hepburn 1952, Morton 1955).

Localities on the mainland of Britain and Ireland have been visited by us and the extent of the populations determined. Information on the populations in the Channel Isles was supplied by a colleague and that for Lundy Isle and Valencia Isle was obtained from previously published data. A survey in 1957 of many areas along the coast of Britain, from North Wales south to Land's End and east to Dungeness, did not reveal any other prostrate populations. Fig. 1 indicates the total known distribution of prostrate forms of *Cytisus scoparius* in the British Isles.

The most northerly site (area 1) for subsp. *maritimus* is near Parwyd on the Lleyn peninsula in North Wales, where there is a small colony at the top of an exposed south-facing cliff extending into the close-grazed Callunetum-grassland on the cliff-top. It is locally abundant on the cliffs in Pembrokeshire (area 2) in South Wales, where it occurs on the south-west coast of the county from St Ann's Head to Eastfield Farm and occasionally as far north as Trevine. The habitat is similar to that in North Wales with the colonies, some of which contain more than 100 plants, extending from the exposed cliff-face back into the vegetation on the cliff-top. On Lundy Isle, off the north coast of Devon (area 3), it is found on the exposed western cliffs (Wright 1933). In Cornwall (area 4) it is locally abundant near the lighthouse at Lizard Point and is also found at Kynance Cove and Gew Graze. At Lizard Point the habitat is similar to that described for North and South Wales. The small colony at Kynance is on a rocky outcrop a little way back from the cliff-top whereas that at Gew Graze, also on a rocky outcrop, is about half a mile inland. Colonies also occur on the east side of the Lizard peninsula on the cliff-face and top south of Carleon Cove and in Downas Valley, where in many places it grows much less prostrate due to heavy competition.

In the Channel Isles, subsp. *maritimus* is locally frequent on exposed south-west-facing cliffs associated with *Calluna*, *Erica* and *Festuca* at Pleimont Point and St Martin's Point in Guernsey (area 5) and at Grosnez Point in Jersey (area 6).

In Co. Cork it grows at Three Castles Head and more extensively at Mizen Head (area 7); both localities are similar in habitat to those in Wales. It is also reported (Scully 1916) as abundant on cliffs at Clynacartan on Valencia Isle, Co. Kerry (area 8).

A further population of prostrate-growing plants exists at Dungeness (area 9)

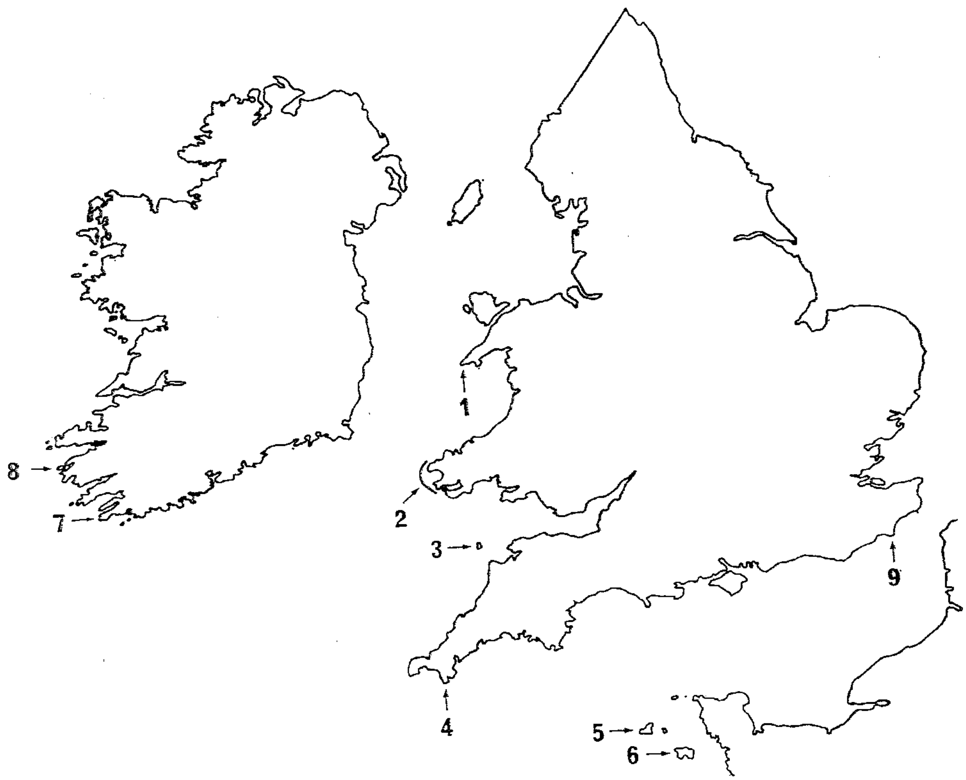

FIGURE 1. Known distribution in the British Isles of the prostrate forms of *Cytisus scoparius*.

in Kent. This habitat is strikingly different from those already described. It comprises more or less flat and very extensive shingle with large numbers of prostrate plants of *Cytisus scoparius* which form the dominant vegetation. Whether the plants in this population are the same as subsp. *maritimus* will be discussed later.

EXPERIMENTAL CULTIVATION OF *CYTISUS SCOPARIUS*

All plants were grown from seed of known wild origin. Seed was sown in August or September in lime-free John Innes Seed Compost. Germination was greatly improved if the seed coat was scratched prior to sowing. The young plants were transferred to pots in a cold frame until the following March or April. They were then planted out in their permanent positions and maintained without competition at the University of Liverpool Botanic Gardens, Ness, Cheshire.

GROWTH HABIT

Subsp. *maritimus* has been distinguished from subsp. *scoparius* on the basis of height (Böcher & Larsen 1958). The degree of hairiness has also been used as a taxonomic character in some Floras, but although subsp. *maritimus* often appears more hairy we have not found this a reliable character. Variation in hairiness of *Cytisus scoparius* creates a large degree of overlap between subsp. *scoparius* and subsp. *maritimus*. We consider that a more useful and complete measure of the variation of growth-habit within the species can be obtained from the ratio $\frac{\text{height}^2}{\text{mean breadth}}\left(\frac{H^2}{\bar{B}}\right)$. This was calculated for all the three-year-old cultivated plants in September 1961. Height was taken as the maximum height above ground level of the tallest shoot, and mean breadth as the average of the greatest and smallest diameters of the plants.

The population at Ness at that time consisted of 88 specimens of subsp. *scoparius* from Britain and Europe, 65 specimens of subsp. *maritimus* (of which 50 originated from Pembrokeshire, eight from Cornwall, five from the Lleyn peninsula, one from Co. Cork and one from Guernsey), and eight plants from Dungeness.

The ratio described above when converted to $\log_{10}$ values gave good separation of the two subspecies on a histogram, with the specimens from Dungeness falling approximately in the middle of the total distribution (Fig. 2). The means and variances of the measurements for the three types are given in Table 1.

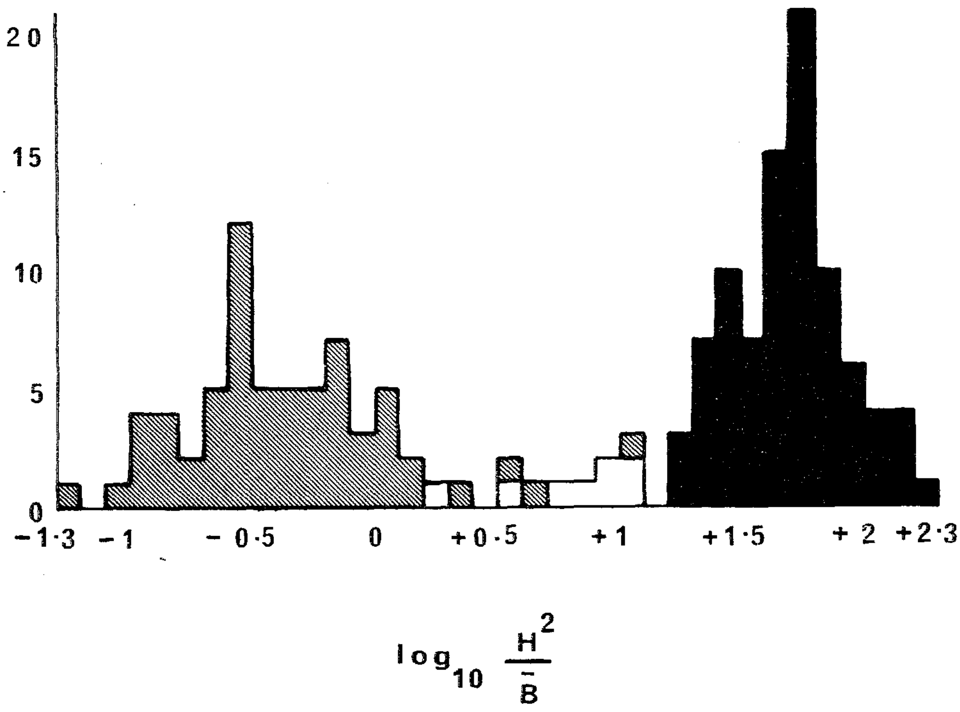

FIGURE 2. Histogram showing separation of the forms of *Cytisus scoparius* using measurement of growth habit.

Solid black area = subsp. *scoparius*.
Shaded areas = subsp. *maritimus*.
Outlined, unshaded areas = Dungeness form.

TABLE 1. MEASUREMENTS OF THREE-YEAR-OLD CULTIVATED PLANTS OF *CYTISUS SCOPARIUS*

	$\log \frac{H^2}{\bar{B}}$		Height in inches		Mean Breadth in inches	
	Mean	Variance	Mean	Variance	Mean	Variance
subsp. *maritimus*	−0·3594	0·1690	4·8923	14·4413	41·9923	198·3086
Dungeness	+0·7999	0·0689	20·1250	30·4107	59·8125	39·7813
subsp. *scoparius*	+1·7171	0·0494	59·9318	279·7195	63·6080	258·8417

In January 1970, further measurements were made of prostrate plants in cultivation. This sample consisted of 51 specimens of subsp. *maritimus* from the various localities mentioned before and 26 plants from Dungeness. The plants were from 3 to 12 years old and the sample therefore approximated more in age structure to a natural population than did the first series of measurements. The results of this second series of measurements are given in Table 2. (The erect subsp. *scoparius* is so obviously different from the two prostrate forms that it was not included in this series).

Measurements of three wild populations, one of each type, were made in 1964 and these are given in Table 3. The population of subsp. *maritimus* was from Pembrokeshire and the sample contained 83 plants. The Dungeness sample

TABLE 2. MEASUREMENTS OF MIXED-AGE CULTIVATED PLANTS OF *CYTISUS SCOPARIUS*

	$\log \frac{H^2}{\bar{B}}$		Height in inches		Mean Breadth in inches	
	Mean	Variance	Mean	Variance	Mean	Variance
subsp. *maritimus*	+0·4632	0·4232	14·4314	82·9302	48·8039	138·4108
Dungeness	+0·9931	0·0906	29·8077	21·3202	79·7692	1474·8846

TABLE 3. MEASUREMENTS OF PLANTS OF *CYTISUS SCOPARIUS* IN WILD POPULATIONS

	$\log \frac{H^2}{\bar{B}}$		Height in inches		Mean Breadth in inches	
	Mean	Variance	Mean	Variance	Mean	Variance
subsp. *maritimus*	+0·1893	0·2702	11·5904	51·4643	52·4650	372·0832
Dungeness	+0·2400	0·0832	12·6400	20·4954	84·3500	699·0530
subsp. *scoparius*	+1·9364	0·0190	68·4833	291·4744	52·9167	396·1880

TABLE 4. STATISTICAL RESULTS SHOWING SIGNIFICANT DIFFERENCES ($p<0{\cdot}05$) BETWEEN THE PROSTRATE FORMS OF *CYTISUS SCOPARIUS* (BASED ON THE RESULTS GIVEN IN TABLES 1, 2 & 3)

	$\log \frac{H^2}{\bar{B}}$		Height in inches		Mean Breadth in inches	
	Variance	Mean	Variance	Mean	Variance	Mean
Cultivated populations (3 years old) subsp. *maritimus* v Dungeness	—	** d = 12·4914	—	** d = 7·8122	* F = 4·985	** t′ = 6·2942
Cultivated populations (varied ages) subsp. *maritimus* v Dungeness	** F = 4·6711	** t′ = 4·8840	** F = 3·8885	** t′ = 9·8320	** F = 10·6558	** t′ = 3·8867
Wild populations subsp. *maritimus* v Dungeness	** F = 2·4573	—	** F = 2·5110	—	** F = 1·8788	** t′ = 9·4131
subsp. *maritimus*, cultivated (various ages) v subsp. *maritimus*, wild	—	—	—	—	** F = 2·6886	—
Dungeness, cultivated (various ages) v Dungeness, wild	—	** d = 12·7578	—	** d = 19·3360	* F = 2·1098	—

*p = 0·05 – 0·01 **p <0·01

contained 100 plants and the population of subsp. *scoparius* came from near Whitchurch in Shropshire, the sample comprising 60 specimens.

An analysis of the three sets of results on the prostrate forms is summarised in Table 4, in which figures are given only for those differences which are significant.

CYTOLOGY

Chromosome studies have been carried out on both mitotic and meiotic preparations. The somatic chromosome number has been determined as $2n = 46$ in 33 specimens of subsp. *scoparius*, 29 specimens of subsp. *maritimus* (from a variety of localities) and 11 specimens from Dungeness. One specimen of subsp. *maritimus* from Cornwall gave a count of $2n = 48$.

Mitotic preparations were obtained from root-tips pretreated for four hours in a saturated aqueous solution of paradichlorobenzene (Meyer 1945), fixed in 1:3 glacial acetic acid : absolute alcohol, stained by the Feulgen method and squashed in 45% acetic acid. Meiotic preparations were obtained from pollen-mother-cells similarly fixed and stained and squashed in iron-acetocarmine (Belling 1926). All preparations were made permanent by the freeze-drying technique (Conger & Fairchild 1953), modified by finally passing through a 1:1 mixture of absolute alcohol : xylene to allow the mounting of preparations in Canada balsam. Meiosis in *Cytisus scoparius* takes place very early in the development of the flower; hence buds for meiotic studies were fixed when about 3–4 mm long and just beginning to show the colour of the petals above the calyx.

The somatic chromosomes of *Cytisus scoparius* (Plates 1a and 1c) are too small for effective karyotyping, being about 1–1·5 μm long after pretreatment with paradichlorobenzene. Most of them are either metacentric or sub-metacentric and, as reported by Böcher & Larsen (1958), two chromosomes carry satellites nearly as large as themselves (arrowed in Plates 1a and 1c). The connection between these satellites and the remainder of the chromosome is frequently very tenuous, so that mistaken counts of $2n = 48$ are easily obtained. The one plant of subsp. *maritimus* from Cornwall which gave a count of $2n = 48$ did show clearly a pair of satellited chromosomes (Plate 1c) so that a mistaken count in this case is unlikely.

Meiosis in all specimens examined was normal with the constant formation of 23 bivalents at metaphase I (Plate 1b). Böcher & Larsen (1958) reported the presence of a single univalent in some of the meiotic cells from a plant of subsp. *maritimus* from Jersey and interpreted this as being indicative of the presence of a trivalent. No evidence of multivalents has been apparent in our investigation. Chromosome segregation was normal at both anaphase I and anaphase II. It was not possible to examine meiosis in the plant with 48 chromosomes, as this count was made from one of a large number of seedlings which were discarded after roots had been fixed.

HYBRIDIZATION

The pollination mechanism of *Cytisus scoparius* has been described by Müller (1883). Essentially it is an explosive mechanism which depends for its effectiveness on the bursting of the anthers and the shedding of their pollen over the immature style and stigma while the flower is still in the bud. The style then elongates so that, when the flower is completely open, it is held under tension. The tension is released suddenly when the sutures of the keel are burst by an insect visiting the flower and the style throws a cloud of pollen above the insect to settle on its back. The stigma rapidly describes a spiral path and, in doing so, first strikes the insect's back where it may pick up pollen from the previous flower visited. It then continues in its path to strike the underside of the insect and possibly pick up pollen deposited there by the short stamens of its own flower.

The existence of this mechanism suggests that emasculation of the flowers prior to the bursting of their anthers would be a necessary preliminary to successful hybridization. All attempts to emasculate flowers however resulted in the buds withering. This also occurred when occlusion of the stigma with a piece of grass culm, a technique found successful in *Lathyrus* (Davies 1957), was substituted for emasculation. Application of various hormone solutions in lanolin to the pedicel following either emasculation or occlusion of the stigma allowed only a low frequency of bud retention to be achieved.

We noted, however, that flowers which remained unexploded or which had been exploded artificially so as to minimise damage to the stigmatic surface set very little seed, although abundant pollen might be present on the stigma. This suggested that some mechanical damage to the stigma is necessary before fertilization can occur.

We therefore gently burst the sutures of the keel by vertically compressing it between the fingers, care being taken to prevent the style from springing. As much as possible of the pollen adhering to the style and stigma was blown off. The stigma was rubbed with forceps to damage it and then cross-pollinated.

In order to test the efficiency of this technique a number of prostrate, yellow-flowered (wild-type) plants were pollinated with pollen from erect cultivars (red- or pale yellow-flowered). Approximately 80% of the progeny were recognised as hybrid, having the habit and flower colour of the cultivars (Table 5).

This series of hybridizations was followed by a number of crosses between the various growth-forms using plants of known wild origin. The results of these crosses are summarised in Table 6. In this Table, plants marked with an

TABLE 5. HYBRIDIZATIONS BETWEEN WILD PROSTRATE AND ERECT CULTIVARS OF *CYTISUS SCOPARIUS*

Female parent		Male parent		Hybrid	
Growth habit	Origin	Growth habit	Flower colour	Growth habit	Flower colour
Prostrate	Guernsey	Erect	Pale yellow	Erect	Pale yellow
Prostrate	Guernsey	Erect	Scarlet wing	Erect	Scarlet wing
Prostrate	Guernsey	Erect	Brick red	Erect	Brick red
Prostrate	Pembrokeshire	Erect	Pale yellow	Erect	Pale yellow
Prostrate	Pembrokeshire	Erect	Scarlet wing	Erect	Scarlet wing
Prostrate	Pembrokeshire	Erect	Brick red	Erect	Brick red
Prostrate	Lizard	Erect	Brick red	Erect	Brick red

TABLE 6. HYBRIDIZATIONS BETWEEN WILD PROSTRATE AND WILD ERECT FORMS OF *CYTISUS SCOPARIUS*

Female parent		Male parent		Hybrid
Grown habit	Origin	Growth habit	Origin	Growth habit
erect	Guernsey	prostrate	Guernsey	prostrate
erect	Guernsey	prostrate	Pembrokeshire	prostrate
erect	Poland	prostrate	Pembrokeshire	prostrate
erect	France	prostrate	Cornwall	prostrate
erect	Switzerland	prostrate	Pembrokeshire	prostrate
erect	Guernsey	prostrate	Dungeness	erect*
prostrate	Dungeness	erect	Ainsdale	prostrate*
prostrate	Pembrokeshire	erect	Poland	prostrate*
prostrate	Pembrokeshire	erect	Spain	prostrate*
prostrate	Pembrokeshire	prostrate	Dungeness	prostrate*

* Putative hybrids awaiting analysis.

asterisk are considered to be hybrid but their certain identification as such must await the analysis of F_2 segregants.

TRANSPLANT EXPERIMENTS

In order to compare survival, resistance to exposure and growth-rate of the erect and prostrate forms of *Cytisus scoparius* in a habitat characteristic of subsp. *maritimus*, 80 plants, each six months old (32 of subsp. *scoparius*, 32 of subsp. *maritimus*, and 16 from the Dungeness locality), were planted out in 1964 on a cliff-face and top near Abermawr in Pembrokeshire. They were planted in mixed groups of five (2 of subsp. *scoparius*, 2 of subsp. *maritimus* and one from Dungeness) to eliminate as far as possible any ecological differences within the area of planting. Seven of these plants are still surviving and all exhibit a prostrate growth habit. However, only five can be identified, for the labels from two have been lost. Four of these are subsp. *maritimus* (none from Dungeness) and the fifth is a low-growing specimen of subsp. *scoparius* from the coast of Britanny. The habit of the two unlabelled plants will be determined by taking cuttings from them and growing at Ness. A further 50 plants of each of the two subspecies were planted out randomly on the cliff in July 1969 and their establishment and growth are being regularly recorded.

Of the seven plants established on the cliff since 1964, only one has so far flowered. This was a specimen of subsp. *maritimus* which flowered after five years, but did not set any seed. This compares with a three-year period before flowering in cultivation.

DISCUSSION

The significant differences in growth-habit between cultivated populations of subsp. *maritimus*, subsp. *scoparius* and the population from Dungeness, all of uniform age, show that all three are genotypically differentiated from each other.

The maintenance of the differences in cultivated populations of mixed ages show that the Dungeness population is made up of plants which are genotypically taller and broader than typical subsp. *maritimus*. The variance of both $\log_{10} \frac{H^2}{\bar{B}}$ and height however is significantly greater in the cultivated mixed-age population of subsp. *maritimus* than in the similar population from Dungeness, suggesting that genotypically the Dungeness population is the more uniform for these characters. The reverse is true for breadth (Tables 2 and 4).

The absence of any difference other than that of variance of breadth between the wild and cultivated (mixed-age) populations of subsp. *maritimus* suggests that this subspecies is strongly canalised to a fairly extreme prostrate growth-habit. The greater variance of breadth in the wild as opposed to the cultivated population may be due to competition in the wild or to the greater age differences within the wild population.

The cultivated mixed-age Dungeness population was significantly taller and had a significantly greater value for $\log_{10} \frac{H^2}{\bar{B}}$ than did the wild population (Tables 2, 3 and 4). This suggests that the population at Dungeness is less rigorously adapted to its particular growth-habit than is subsp. *maritimus* and so suffers some degree of kill-back of upright shoots in the wild. The absence of any differences in variance, however, of either height or $\log_{10} \frac{H^2}{\bar{B}}$ between wild and cultivated populations must be a function of all plants in the wild suffering equal exposure and therefore all being killed back to a similar height. As the habitat at Dungeness is very homogeneous this effect might be expected.

There is no difference in either mean height or mean $\log_{10} \frac{H^2}{\bar{B}}$ between the wild subsp. *maritimus* and the population growing at Dungeness. The action of the environment is therefore causing the Dungeness population to mimic subsp. *maritimus*. The greater variance of height and of $\log_{10} \frac{H^2}{\bar{B}}$ in subsp. *maritimus* is probably due to the extreme heterogeneity of the Pembrokeshire habitat in comparison with that at Dungeness. The greater variance in breadth of the Dungeness population compared with subsp. *maritimus* may be due to the absence of competition on the beach at Dungeness allowing the breadth of any specimen to be limited only by its own capacity for lateral growth. The breadth of the specimens at Pembrokeshire is most likely governed by competition with other species, in particular *Calluna vulgaris*.

The chromosome number of *Cytisus scoparius* has been determined as $2n = 46$ with the exception of a single plant of subsp. *maritimus* from Cornwall which gave a count of $2n = 48$. This confirms the observations of Böcher & Larsen (1958). We also agree with these authors that many of the reported counts of $2n = 48$ probably arose from the misidentification of the two large satellites as a separate pair of chromosomes. It is extremely difficult to account for the single reported count of $2n = 24$ (Morton 1954). Not only is his count at variance with all others, but the chromosomes which he illustrates are much larger than those shown by Böcher & Larsen or those seen by us. The longest chromosome illustrated by Böcher & Larsen is approximately 1·5 μm, which agrees with our observations, whereas in Morton's illustration the shortest chromosome is about 1·5 μm and the longest is about 4·5μm. This must raise some doubts about the correct identification of Morton's material.

No internal barriers to hybridization are apparent between prostrate and erect forms of *Cytisus scoparius*. The results of confirmed crosses between prostrate forms and erect cultivars are different from those between prostrate forms and erect wild plants (Tables 5 and 6). Whereas in the former the hybrid plants are erect, in the latter they are prostrate. This difference in the expression of the genes controlling growth-habit between two crosses suggests that the horticultural coloured varieties of *Cytisus scoparius* are of hybrid origin and contain, as well as genes causing alternative colour development in the flower, genes governing growth habit which do not normally occur in wild *Cytisus scoparius*.

The results of the transplant experiments so far analysed show that the selection acting against the establishment of any other ecotype of *Cytisus scoparius* in the natural habitat of subsp. *maritimus* is extremely strong, and causes the elimination of very large numbers of young plants even when these are planted out at a stage which overcomes any competition for initial establishment.

The evidence so far accumulated suggests that *Cytisus scoparius* exists as two quite distinct growth-forms and that these erect and prostrate forms are easily distinguishable. The prostrate type in Britain is represented by subsp. *maritimus*, which occurs on various exposed sea-cliffs, and by the prostrate population on the shingle beach at Dungeness. There is no chromosomal difference between the various forms, all having $2n = 46$. The Dungeness population, although referable in the field to subsp. *maritimus*, behaves differently from this subspecies in cultivation and has thus been shown to be genetically distinct from subsp. *maritimus*.

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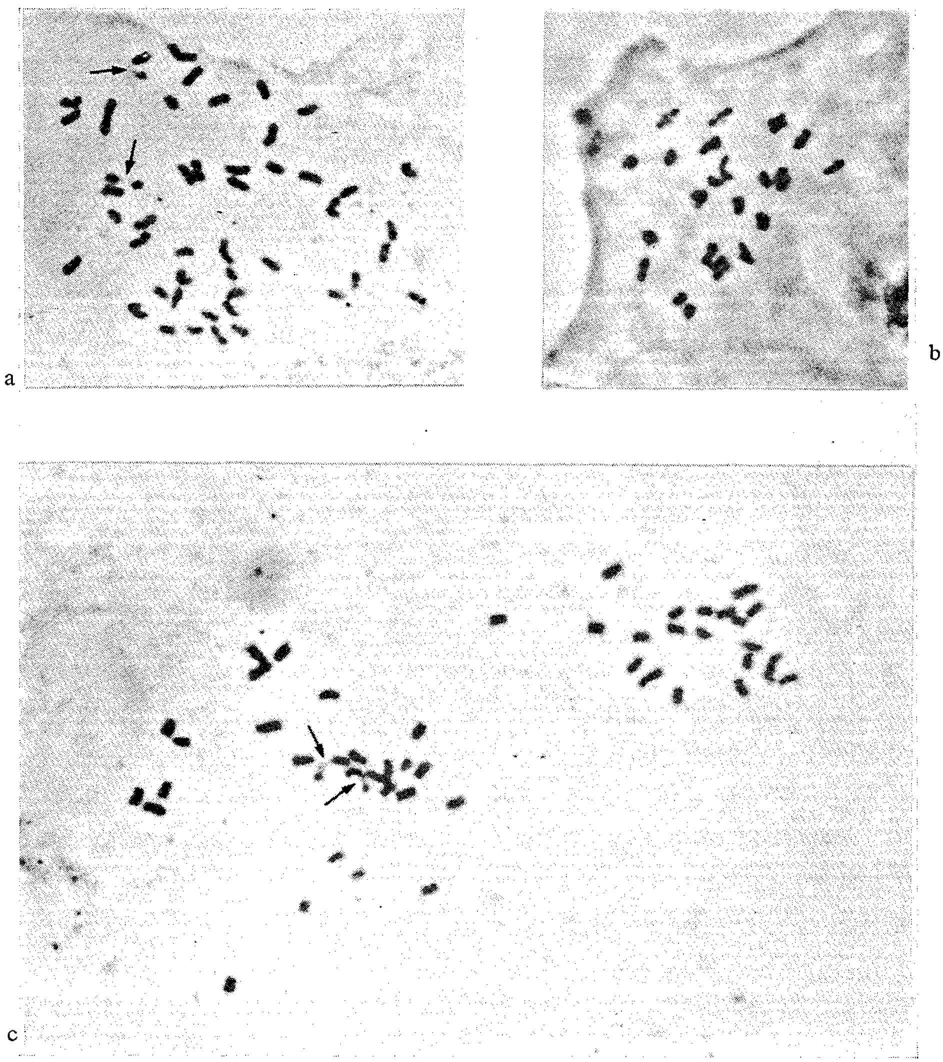

PLATE 1. Chromosomes of *Cytisus scoparius* (all × 1600).

a. Root mitosis showing $2n = 46$ including two satellited chromosomes (arrowed).
b. Meiosis showing 23 bivalents.
c. Root mitosis showing $2n = 48$ including two satellited chromosomes (arrowed).