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An upland race of *Potentilla erecta* (L.) Räusch. in the British Isles

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ABSTRACT

Plants of *Potentilla erecta* from three different environments in Scotland showed considerable phenotypic differences. After cultivation in standard conditions those from dwarf-shrub communities at about 800 m retained a number of distinctive features. A survey of some herbaria disclosed that similar plants are widespread and not uncommon above 500m in the British Isles and are identical with *Potentilla strictissima* Zimm. from the Alps. The new combination *Potentilla erecta* (L.) Räusch. subsp. *strictissima* (Zimm.) A. J. Richards is made for this taxon, and its origin and status are discussed. Both this subspecies and *P. erecta* subsp. *erecta* proved tetraploid ($2n = 28$). In one locality where they occur together some intermediates were found.

INTRODUCTION

Potentilla erecta is widespread in the British Isles and is often very common in acid habitats, being found in grassland, heath, mire and woodland. It is also less commonly found in base-rich grassland and fen. It is not surprising that considerable inter-population variability is found, although intra-population variability is usually slight. Some of the more extreme variants on the Continent have been given taxonomic recognition, e.g. *P. sylvestris* Necker, *P. pubescens* Poeverlein, *P. favrati* Zimm. and *P. strictissima* Zimm. A number of other variants were given infraspecific recognition as *varietas* and *forma* by Zimmeter (1884, 1889) and Wolf (1908), and the complex infraspecific taxonomy of *P. erecta* was usefully summarised by Hegi (1922), who listed no fewer than 19 taxa (excluding synonyms) under this species. Recent work has been published on the experimental hybridisation and genetic relationships of *P. erecta* with related species (e.g. Matfield *et alii* 1970), and Vasari (1968) and Watson (1969) both reported the experimental testing of phenotypes of *P. erecta* in cultivation.

This paper reports the occurrence of a distinct genotype of *P. erecta* from dwarf-shrub heaths usually above 500m altitude in the British Isles, apparently identical with *P. strictissima*. Chromosome counts of both this taxon and the commoner one (*P. erecta* subsp. *erecta*) are reported and the origin and ecology of both are discussed.

CULTIVATION EXPERIMENTS

MATERIAL

Three Scottish populations were chosen for detailed examination in August 1968

(Table 1). Measurements were made in the field and plants were removed and grown in constant conditions at Oxford.

TABLE 1. ORIGIN OF MATERIAL USED IN CULTIVATION EXPERIMENTS

Population	Locality	Habitat	No. sampled In field	No. sampled In cultivation
Calgary	Calgary Bay, Mull, Scotland GR 17/372.512	Grassland on shell-sand 5m	50	13
Kilbrenan	Kilbrenan, opposite Ulva, Mull, Scotland GR 17/444.423	Wet peaty grassland 50m	50	27
Cairngorm	White Lady, Cairn Gorm, Inverness, Scotland GR 28/992.055	Dwarf-shrub heath 780m	47	16

METHOD

Four characters were scored in the field from about 50 flowering individuals chosen without conscious bias. These were length of plant, length of stem-leaf, length of fruiting pedicel and length of petal (Table 2).

TABLE 2. CHARACTERS SCORED ON WILD AND CULTIVATED POPULATIONS

Definition of characters

Length of longest stem from flower to ground (fully extended)
Length of longest leaflet from base to apex on uppermost stem-leaf
Maximum breadth of (same) longest leaflet
Length of terminal tooth of (same) longest leaflet
Length of longest leaflet on longest radical leaf
Maximum breadth of (same) longest radical leaflet
Length of petiole of (same) longest radical leaf
Whether or not leaflets of basal leaf overlap
Colour of basal leaf, scored as blue-green, green or yellow-green
Length of longest petal of largest flower from notch in emarginate apex to base of claw
Length of longest fruiting pedicel

Plants taken into cultivation were grown in 4-inch plastic pots in John Innes soil mixture No. 3. They were subjected to illumination from mercury-vapour lights for 14 hours out of 24 and were maintained at a fairly constant temperature of about 18°C. Characters were scored on these plants when they first flowered and fruited, in June–August 1969, 10–12 months after transplantation. These plants were kept in cultivation for a further year but no subsequent phenotypic change was noted and it was assumed that phenotypic differences noted in cultivation were under genetic control. In all, 12 characters were scored (Table 2).

RESULTS

Each population is compared before and after cultivation by means of histograms for each character:

Length of longest stem (Fig. 1). The plants of the Cairngorm population are substantially larger in the field than those of the two lowland populations. This distinction is maintained, albeit less clearly, after cultivation. The larger size of plants of the Calgary population in relation to those of the Kilbrenan one in the field is not maintained in cultivation.

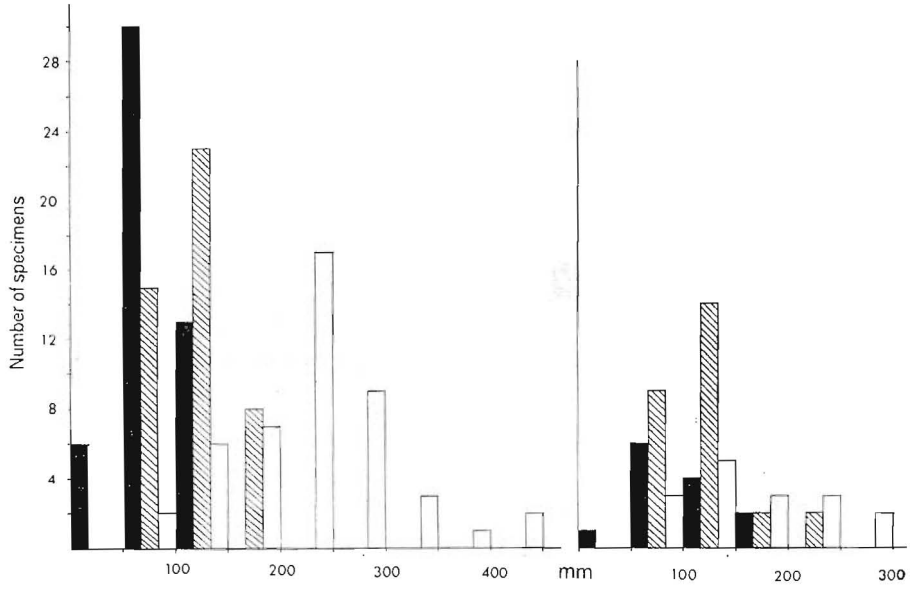

FIGURE 1. Length of longest stem. Left, field results; right, after transplantation. Black, Kilbrenan; hatched Calgary; unshaded, Cairngorm.

Length of uppermost stem-leaf (Fig. 2). Plants of the Cairngorm population in the field have much longer stem-leaves than the two lowland populations. This distinction is maintained after cultivation. The larger stem-leaves of the Calgary population in the field in relation to those of the Kilbrenan one are not maintained in cultivation.

Length of fruiting pedicel (Fig. 3). The greater length of the pedicels of plants of the Cairngorm population in the field is at least partly lost after cultivation. The Calgary and Kilbrenan populations do not differ in cultivation.

Petal-length (Fig. 4). The much longer petals displayed by the Cairngorm population in the field are maintained in cultivation. However, the lowland populations show increased petal-length after cultivation and become indistinguishable from the Cairngorm population in this character.

The length of petiole, breadth of stem-leaf leaflet, breadth of radical leaf leaflet, and length of terminal tooth were found not to differ after cultivation. The qualitative characters (colour and overlapping) were found to be difficult to score and were not employed in the final analysis. The length of the radical leaf,

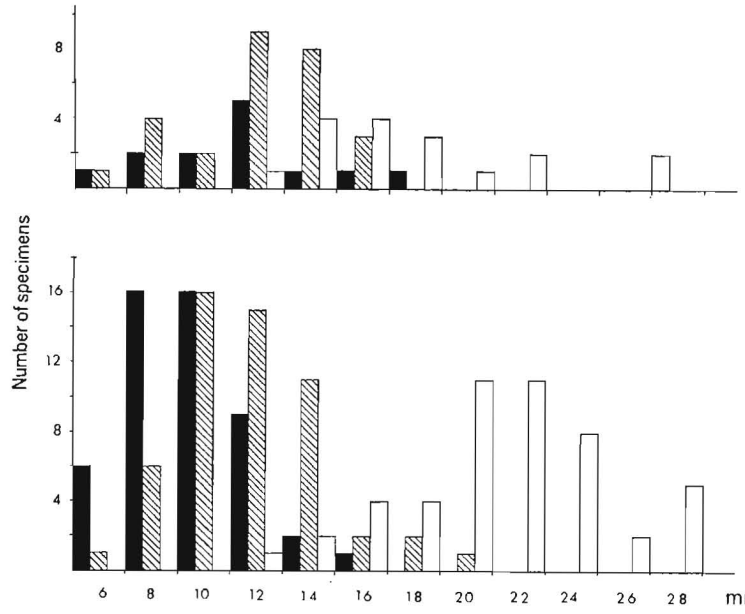

FIGURE 2. Length of uppermost stem-leaf. Below, field results; above, after transplantation. Key as in Fig. 1.

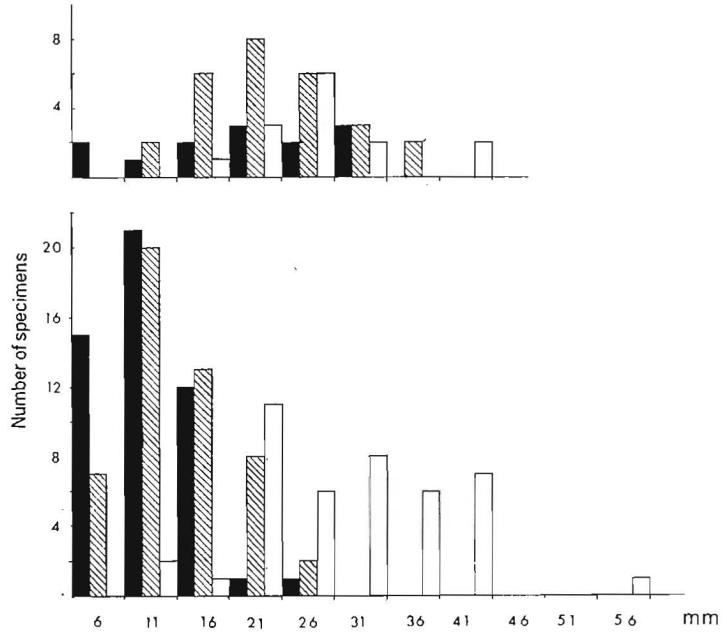

FIGURE 3. Length of fruiting pedicel. Below, field results; above, after transplantation. Key as in Fig. 1.

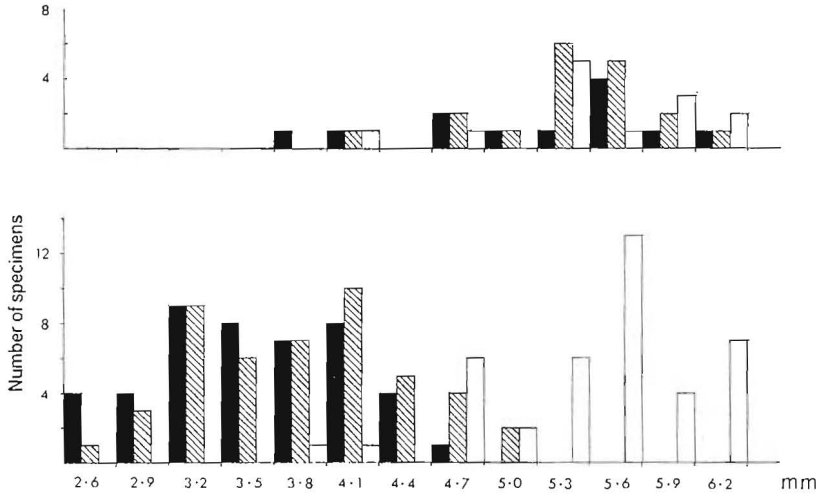

FIGURE 4. Petal-length. Below, field results; above, after transplantation. Key as in Fig. 1.

although not recorded in the field, was found to be a discriminant between the Cairngorm and the two lowland populations after cultivation.

In conclusion, it can be said that the Cairngorm population can be distinguished from the two lowland populations through several characters in the field, and that these are maintained, although usually less distinctly, after cultivation (Table 3). The lowland populations are scarcely separable in the field through the biometric techniques employed here, although they looked quite distinct to the eye, and both biometrically and visually they became indistinguishable after cultivation.

TAXONOMY AND DISTRIBUTION

The cultivation experiment established that an upland population of *Potentilla erecta* from Scotland remained distinct from two lowland populations with respect to several characters, and thus apparently constituted a recognisable ecodeme. Consequently, a search was made in the Druce Herbarium, Oxford (**OXF**), to determine whether phenotypes similar to the Cairngorm population could be found elsewhere in the British Isles. Three different collections were found apparently corresponding to this ecodeme, two from the Cairngorm range of mountains and one from about 500 m in Brecon (central Wales), the latter annotated by Wolf. As a result the search for similar phenotypes was extended to the British Museum (**BM**), where a number of other collections was found that apparently agreed with the Cairngorm population. The localities were plotted on the 10 km square grid of the Ordnance Survey and a map was produced with the assistance of the Biological Records Centre at Monkswood, Huntingdonshire (Fig. 5). This is compared with an updated version (Fig. 6) of the map of *Potentilla erecta* published in Perring & Walters (1962). All stations of the upland ecodeme are in upland areas of the British Isles, and most are above 500 m (about 1600ft) (Table 4).

TABLE 3. CHARACTERS IN WHICH LOWLAND AND UPLAND POPULATIONS OF *POTENTILLA ERECTA* DIFFER

IN THE FIELD	AFTER CULTIVATION
Lowland (Calgary, Kilbrenan)	*Lowland (Calgary, Kilbrenan)*
plant less than 150 mm in total length	plant less than 200 mm in total length
stem-leaf less than 16 mm in length	stem-leaf less than 18 mm in length
fruiting pedicel less than 25 mm in length	fruiting pedicel less than 30 mm in length
petal less than 4·5 mm in length	not separable from upland populations
plant weak and often decumbent	plant weak and decumbent
leaves not coarsely dentate; teeth rarely exceeding 1·5 mm in length; leaves dentate to ½ way	leaves not coarsely dentate; teeth variable in size
stipules less than 10 mm in length, divided to ½ way	stipules less than 10 mm in length, divided to ½ way
Upland (Cairngorm)	*Upland (Cairngorm)*
plant usually more than 150 mm in total length	plant usually more than 150 mm in total length
stem-leaf usually more than 16 mm in length	stem-leaf usually more than 14 mm in length
fruiting pedicel usually more than 20 mm in length	fruiting pedicel usually more than 20 mm in length
petal usually more than 4·7 mm in length	not separable from lowland populations
plant stiffly erect	plant erect
leaves coarsely dentate; teeth usually exceeding 1·5 mm in length; leaves dentate to base	leaves coarsely dentate; teeth always exceeding 1·0 mm in length
stipules usually exceeding 10 mm in length, divided nearly to base	stipules more than 10 mm in length, divided nearly to base

TABLE 4. LOCALITIES FOR THE UPLAND ECODEME OF *POTENTILLA ERECTA* IN THE BRITISH ISLES

v.c. 42 Brecon, Llanwrtyd Wells. G. C. Druce. No date. **OXF**
v.c. 48 Merioneth, near Barmouth. H. W. Mornington. July 1890. **BM**
v.c. 64 Mid-W. Yorks., near Grassington. T. J. Foggitt. 24 June 1922. **BM**
v.c. 66 Durham, Widdybank Fell, GR 35/817.295. A. J. Richards. 29 July 1971. **OXF**
v.c. 81 Berwick, pathside near Rathburne Ford. E. B. Bangerter. 1 August 1960. **BM**
v.c. 90 Forfar, rocks above Loch Brandy, 2300 ft. A. H. G. Alston. 6 July 1947. **BM**
v.c. 95 Elgin, woods of Castle Grant, Grantown-on-Spey. C. Bailey. 25 July 1895. **OXF** (two sheets)
v.c. 96 Easterness, Boat of Garten. G. C. Druce. 1888. **OXF**
v.c. 96 Easterness, Coire an Lochan, near Loch, Cairngorm, GR 28/982.028. A. Melderis. 1 July 1953. **BM**
v.c. 96 Easterness, near White Lady Shieling, Cairn Gorm, GR 28/992.055. A. J. Richards. **OXF**
v.c. 98 Argyll, Dalmally. G. C. Druce 1885. **OXF**
v.c. 106 Ross, Fannich. H. J. Riddelsdell. July 1902. **BM**
v.c.H12 Wexford, between Mount Street, Benedict and Croonford. A. H. G. Alston. 27 June 1952. **BM**
v.c.H29 Leitrim, Glenade Cliffs. W. C. Barton. 18 August 1913. **BM**

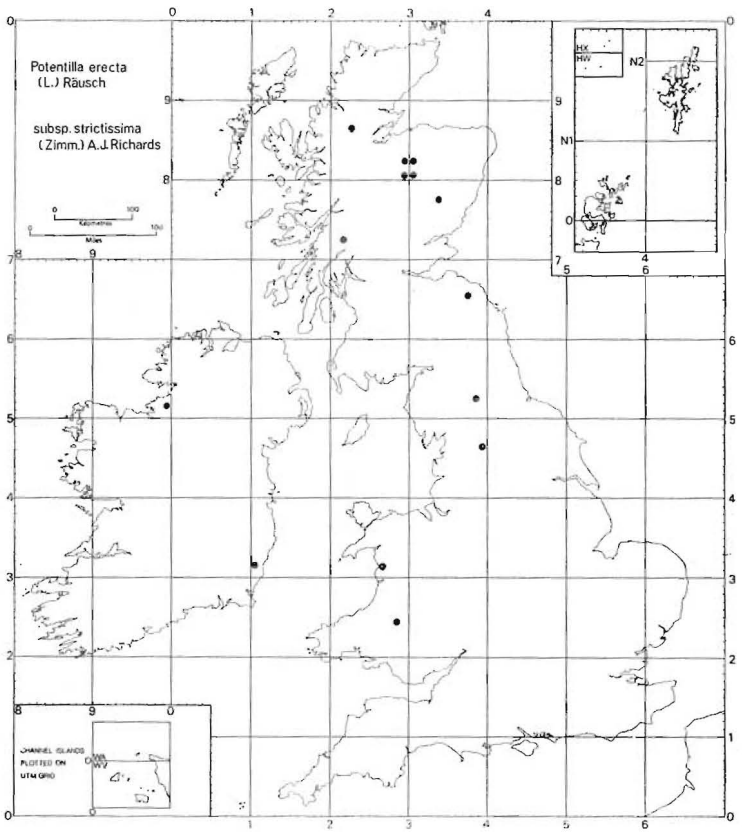

FIGURE 5. Distribution of *P. erecta* subsp. *strictissima* in the British Isles.

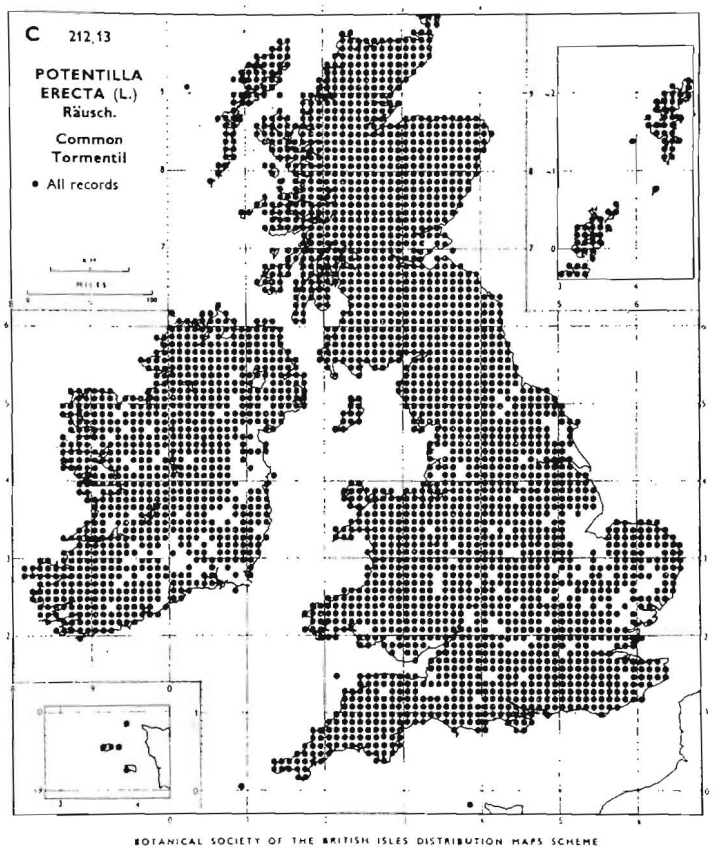

FIGURE 6. Distribution of *P. erecta* in the British Isles.

In all cases the upland ecodeme could be identified by means of the characters listed in Table 3. In a few cases it was not possible to assign a specimen to the lowland or upland ecodemes, but in the great majority the two seemed clear-cut (Figs. 7 & 8).

At this stage in the investigation it appeared that an upland ecodeme, distinct in a number of characters from lowland ecodemes and remaining distinct after cultivation, occurred in a number of widespread localities (and possibly not

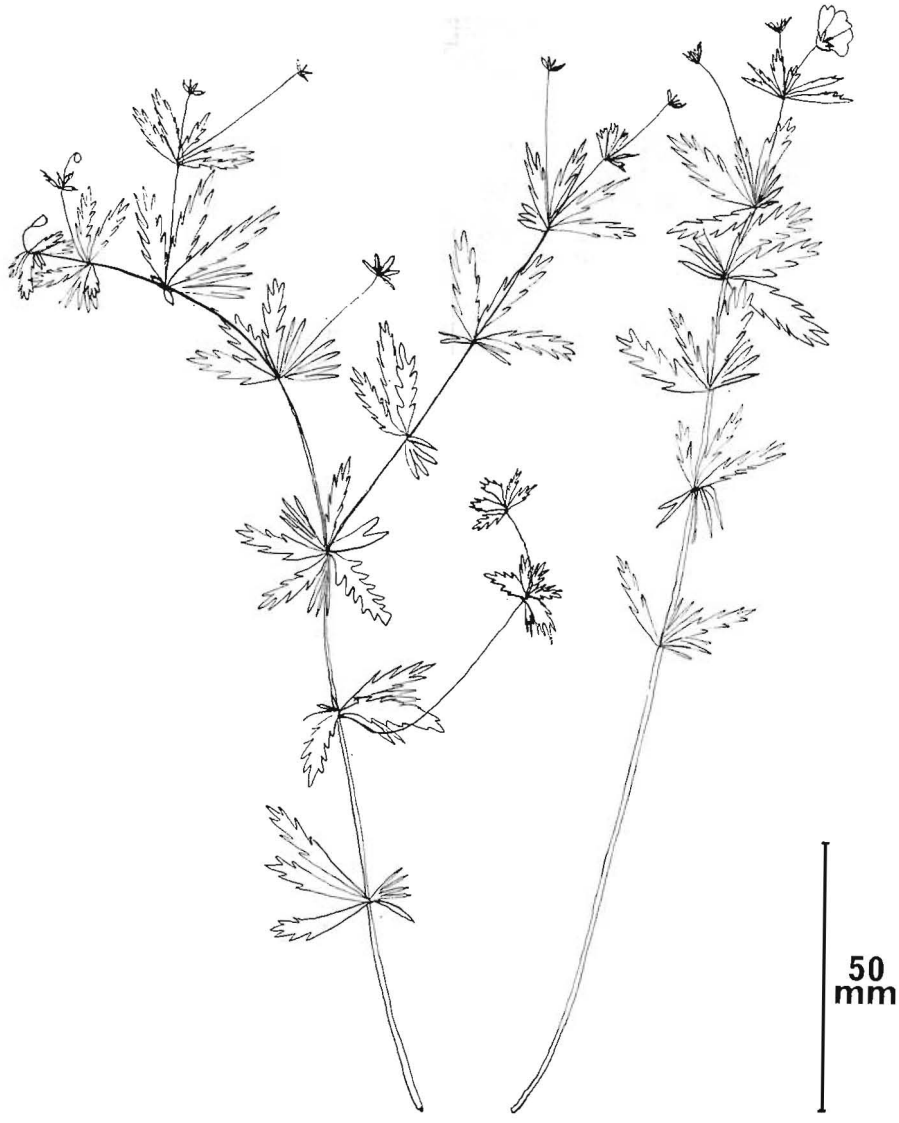

FIGURE 7. *Potentilla erecta* subsp. *strictissima*. Drawing of specimen from **BM**: Rocks above Loch Brandy, Forfar, Scotland, 2300 ft, 6th July 1947. A. H. G. Alston. Annotated by Alston: "approaches var. *strictissima*".

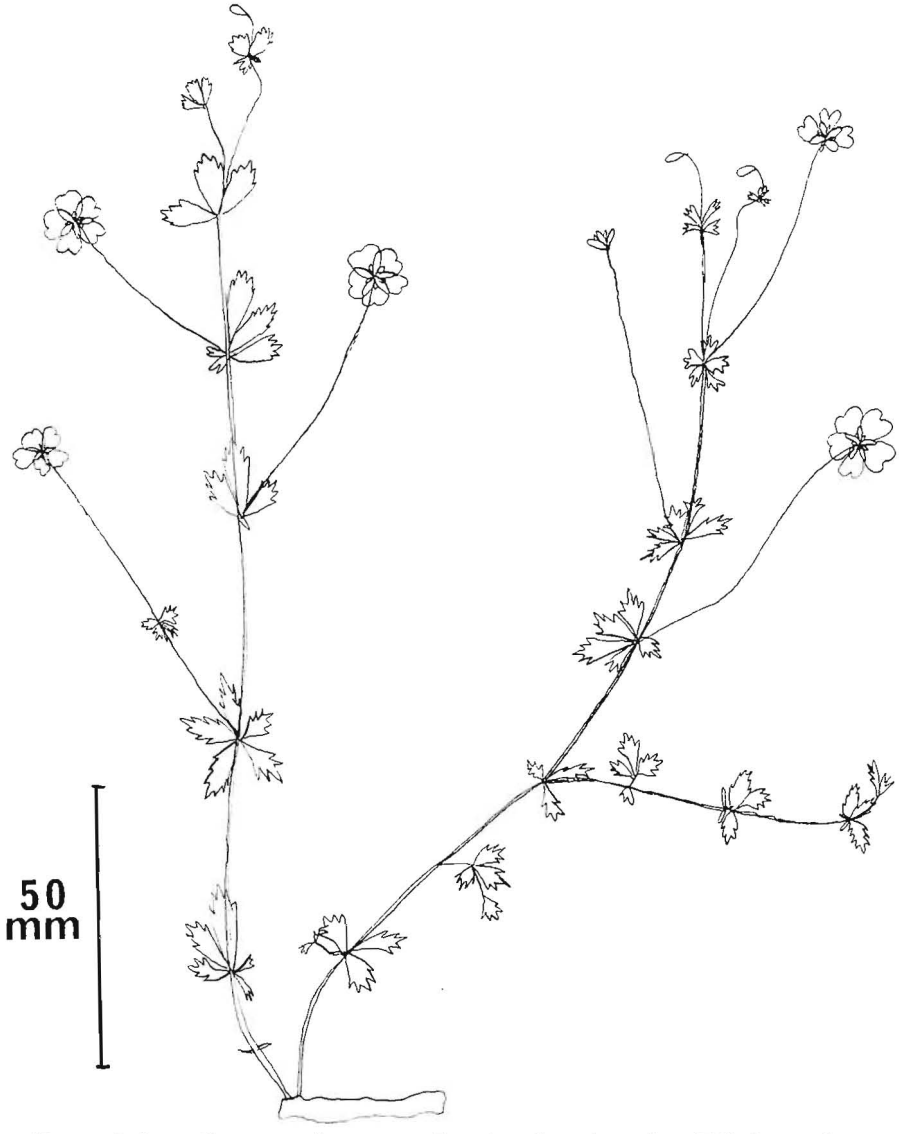

FIGURE 8. *Potentilla erecta* subsp. *erecta*. Drawing of specimen from **BM**: In wood on chalk, Funtingdon, Sussex, England, 14th June 1931. R. Meinertzhagen.

uncommonly) above 500 m in the British Isles, perhaps usually in dwarf-shrub communities. It seemed that this ecodeme was worthy of taxonomic recognition at the subspecific level, so it was necessary to discover whether a similar phenotype had been described elsewhere.

Two British specimens of this ecodeme had been identified as *Potentilla erecta* var. *strictissima* (Zimm.) Hegi, namely:

1. Brecon, Llanwrtyd Wells. *G. C. Druce*. **OXF**. This specimen is annotated

by T. Wolf: '*Potentilla tormentilla* (Crtz.) Neck. var. *strictissima* (Zimmeter) Focke, quae flores habet multo majores quam aliae varietates'.
2. Forfar, rocks above Loch Brandy, 2300 ft. *A. H. G. Alston.* 6 July 1947. **BM.** This is annotated by Alston: 'approaches the var. *strictissima* (Beck) Focke in Wolf's key on p. 645 of the monograph'. (Fig. 7).

It appears that the former record is responsible for the inclusion of var. *strictissima* by Druce (1928) in his *British Plant List.* Both specimens closely match material of the Cairngorm population as it appears in the field. The basionym of *P. erecta* var. *strictissima* seems to be *P. strictissima* Zimmeter (1884, p. 5), the original description of which is as follows:

'Caudiculis stricte erectis, apice tantum dichotomis, paucifloris, ramis non divergentibus, foliolis oblongo-lanceolatis, sessilibus, magnis, interdum aliquantulum sericeis, incise et acute serratis; stipulis magnis profunde incisis, incisuris lanceolatis'.

My translation of this Latin description is:

'Stems rigidly erect with the apex somewhat dichotomously branched, few-flowered, with the branches not spreading; leaflets oblong-lanceolate, sessile, large, sometimes somewhat sericeous, deeply and sharply serrate; stipules deeply divided with lanceolate divisions'.

This description might refer to the Cairngorm population, but is somewhat vague as to the essential features of this variant. However, in Hegi (1922, p. 883) there is a German description of *Potentilla erecta* var. *strictissima* (Zimm.) Hegi, which translates as follows: 'Stem strong, mostly erect, to 50 cm, simple or 1–2-branched only in upper part, few-flowered. Leaflets large, to over 3 cm long, sessile, coarsely dentate, sparsely or moderately hairy, often glabrescent above, often densely hairy on nerves below. Bracts often over 2 cm long, deeply 3-partite. Petals large, considerably exceeding sepals'.

This description resembled that of the Cairngorm population closely and I felt it worthwhile obtaining authentic material of *P. strictissima.* I have been unable to trace any material collected by Zimmeter, but a specimen at the Botanical Museum, Zürich University (**Z**), was collected by H. Siegfried in June 1884; it was checked by Zimmeter, who acknowledged the collector when he published *P. strictissima* in November 1884. This specimen (Fig. 9), which is very similar to the Cairngorm population, is here selected as the lectotype for *P. strictissima.* The details are as follows:

Potentilla strictissima Zimm., teste A. Zimmeter. Hoch. Wülflingen, *c* 550m [near Winterthur, Switzerland], 13.6.1884. *H. Siegfried.* **Z.**

A search in the European herbarium at **BM** revealed a further eighteen specimens similar to the British upland ecodeme, including seven labelled *P. strictissima,* and there are eight specimens at the Botanical Museum of the Technical High School, Zürich (**ZT**), also labelled *P. strictissima,* which closely resemble the British plant. They include two exsiccatae:

1. *Potentilla strictissima* Zimmeter. Tirolia australis: in locis fruticosis apricis vallis 'Vestino' in Judicaria. Solo calcareo. 15.7.1893. *P. Porta.*
2. Flora Exsiccata Austro–Hungarica 2836. *Potentilla strictissima* Zimmeter.

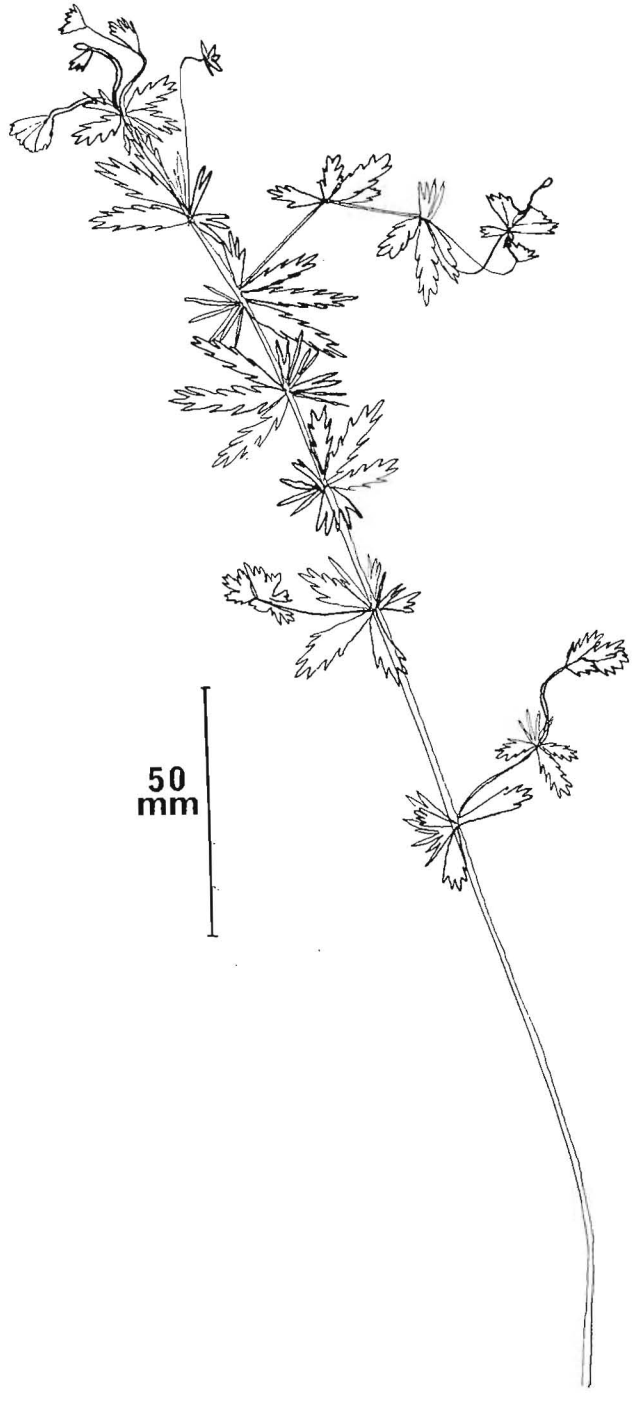

FIGURE 9. *Potentilla erecta* subsp. *strictissima*. Drawing of part of lectotype specimen (for details see p. 310).

Austria superior. Ad ripas graminosas rivi 'grosser Weissenbach' prope pagum Reichramring. *Steininger.*

Although there is little doubt that the upland ecodeme of *P. erecta* in the British Isles is the same as *P. strictissima*, there being a very close resemblance to and no important differences from the lectotype, other Continental material, and Hegi's description, there remains the question of the taxonomic rank to which it should be referred. It is clear that it is genetically distinct from lowland plants with regard to several morphological characters and that it is ecologically and geographically distinct, at least in the British Isles. Thus, it would seem to warrant a higher rank than varietas. The distinction between species and subspecies can be a delicate one, in which much is left to the taste of the taxonomist. In the present case, it appears that interbreeding between the ecodemes can and does occur on occasions (see below), and there is no indication that a barrier to gene-exchange exists apart from that imposed by habitat differences. Although several character differences are found, these are quantitative, and both ecodemes would seem to fall into the same species when interspecific differences in the remainder of section Potentilla are considered. In fact I see no reason why subspecies should not be adopted in the circumstances, although opinions have differed in the past, and may well differ in the future.

I have examined the sheet of *Tormentilla erecta* in the Linnaean herbarium in London (**LINN**). There are three specimens, one larger than the others, but all clearly belong to the lowland British ecodeme and are quite different from subsp. *strictissima*. Thus the lowland British ecodeme is subsp. *erecta*.

As a result I have decided to make the following new combination:

POTENTILLA ERECTA (L.) Räuschel
Subsp. STRICTISSIMA (Zimmeter) A. J. Richards, **comb. et stat. nov.**
Potentilla strictissima Zimmeter, Europ. Art. Potentilla, p. 5 (1884)
Potentilla erecta var. *strictissima* (Zimmeter) Hegi, Illustrierte Flora von Mittel-Europa, **4**: 883 (1922)

Subsp. *strictissima* differs from subsp. *erecta* as follows (Figs. 7 & 8):

Plant stiffly erect, usually exceeding 150 mm in maximum length. Stem-leaves coarsely and acutely serrate to base, usually exceeding 20 mm in length; radical leaves coarsely and obtusely serrate, leaflets oblong-lanceolate to obovate; stipules long, usually exceeding 10 mm, divided almost to base. Peduncles exceeding 20 mm in fruit, erect, stiff. Flowers sparse, exceeding 11 mm in diameter; petals exceeding 4·5 mm in length.

Dwarf-shrub heath, or less commonly in grassland, on peat or mineral soils, usually above 500 m in the British Isles. Not uncommon, and doubtless under-recorded at present, but apparently local: Brecon, Merioneth, Mid-W. Yorks., Durham, Berwick, Scottish Highlands from Argyll to W. Ross, Wexford and Leitrim (Fig. 5, Table 4).

It is recorded in the literature from much of the European range of *P. erecta* subsp. *erecta*, although only a thorough survey of the herbaria would reveal to what extent these records are correct. Literature records have been traced from Austria, France, Germany, Hungary, Italy, Sicilia, Poland, Switzerland, Jugoslavia and several districts of the U.S.S.R., including the Ukraine, Caucasus, central Urals and parts of Siberia. In most areas it seems to be alpine or sub-

arctic in distribution, being mostly restricted to high mountains in central Europe although intergrading with subsp. *erecta* at lower altitudes (Hegi 1922). I have examined the European collection at **BM**, where specimens from the following countries agree with subsp. *strictissima*: Austria, Belgium (at 250 m), Bulgaria, Finland, Norway, Sweden, Poland and the Ukraine.

I became acquainted with the work of Vasari (1968) after I had reached the tentative conclusion that the British upland ecodeme merited subspecific status and that subsp. *strictissima* would be its correct name. I was thus very interested to find that Vasari, who had conducted a very thorough genecological survey of *P. erecta* in Finland, had reached similar conclusions about the race from isolated bog habitats in northern Finland, which is north of the main distribution of the species in that country. Like Juzepczuk (1959), Vasari (1968) suggested that this race may be referable to *P. strictissima*, as, following the description given by Wolf (1908), it shares with that species a low degree of branching, a small number of flowers, leaves which are longer than 3 cm and tend to be glabrous, and a red stem. However, he pointed out that the Finnish race is much smaller than *P. strictissima*. From the characters mentioned, and from his Fig. 7, it seems that this northern race cannot be placed here, and Vasari (pers. comm., 1972) now concurs with this opinion. Further, a number of the points in the descriptions of Hegi and Zimmeter (for instance: large flowers; strong, erect, rigid stems; sharply and deeply serrated leaves; and large, deeply divided stipules) were not mentioned by Vasari, although these characters are all typical of the upland British plant. In fact, the plant illustrated by Vasari in his Fig. 6 as the *southern* Finnish race bears a strong resemblance to subsp. *strictissima* and may well be referable to this taxon. I have found herbarium material of subsp. *strictissima* from a number of localities in southern Finland, Sweden and Norway at **BM**. Vasari (pers. comm.) suggests, no doubt rightly, that the northern Finnish race is a new subspecies, and agrees that most of the southern race can be referred to subsp. *strictissima*, although plants from the southern extremity of Finland seem to be subsp. *erecta*.

CYTOLOGY

There are published chromosome counts of *P. erecta* from the British Isles, Holland, Iceland, Finland and Poland. In all cases $2n = 28$, a tetraploid count, is reported. I can find no chromosome reports of plants which from morphological or ecological considerations might be subsp. *strictissima*, and it was decided to examine some British material of both subspecies.

MATERIAL

Plants were collected under licence from *Calluna* heath on peat at 1650 ft (500 m) on Widdybank Fell, Upper Teesdale, Co. Durham, England, during July 1971. This site was chosen partly for convenience and partly because both subspecies appear to grow together at this station (no other site is at present known in Britain where this occurs).

METHOD

The plants were potted in John Innes No. 3 compost and were grown in a greenhouse. After two months they were sufficiently established for root-tips to be

examined. These were excised and pretreated in a saturated solution of 1-bromonaphthalene for 2 hours. They were fixed in a freshly made mixture of 3:1 (v/v) absolute alcohol: glacial acetic acid overnight and hydrolysed for 8 minutes in normal HCl at 60°C. Staining in Feulgen Reagent for 2 hours preceded squashing in acetocarmine.

RESULTS

Useful preparations were obtained for 9 individuals. 4 of these were referable to subsp. *strictissima*, 3 to subsp. *erecta* and 2 were intermediate. In all 9 the count $2n = 28$ was recorded. Several cells were examined from each of 2 to 4 root-tips per individual and, in all, some 75 cells were examined. No cytological variation was observed. The chromosomes are small (1·0–1·4μm in length) and rather characterless.

DISCUSSION

It will be clear that the investigations reported here were not designed as a thorough genecological survey of *Potentilla erecta*. The experiments were intended as a preliminary investigation, but from these arose data of taxonomic interest which were considered to merit publication. Much more thorough genecological surveys have been published by Vasari (1968) and Watson (1969), and cytogenetic surveys by Matfield *et alii* (1970). The sample sizes employed in the present survey were too small for statistical treatment and no study was made of filial populations. However, it is instructive to consider the present report in the light of previous work.

Watson (1969) showed that genetic differentiation may occur in *P. erecta* over very small distances (about 5 m) at a sharply defined ecotone and concluded that differentiation is maintained through contrasting selection pressures in adjacent habitats, and is aided by habitat conservatism in pollinators. She pointed out that *P. erecta* is entomophilous and self-incompatible, requiring cross-pollination for reproduction to occur. Nevertheless, analysis of families grown from seed showed that some considerable gene-exchange occurred between individuals in different habitats. Watson's populations came from Scotland (the altitude is not mentioned), but were not from dwarf-shrub communities. Of the character discriminants reported in the present work, only plant-length was found by Watson to differ between habitats, and the other characters that she found to differ are probably developmentally linked to plant-length, as she herself commented. However, Watson's work is important in the present context in demonstrating that *P. erecta* is a variable species that readily undergoes genotypic differentiation. It should be noted that the Calgary and Kilbrenan populations in the present study show no such differentitation after cultivation.

Vasari (1968) also demonstrated some genotypic differentiation, but in this case it was dominated by a clear-cut difference in 5 characters (none of which has been examined quantitatively in the present study) between southern and northern populations in Finland. These characters are:

the branching of the stem and inflorescence
anthocyanin coloration (not varying in British material)
length/breadth ratio of terminal leaflets (measured in British material but

discounted in favour of length alone)
hairiness of leaflets
number of styles per flower.

It would appear that most of Vasari's southern race may be referable to subsp. *strictissima*. This race he finds common and widespread in a clearly demarcated zone of southern Finland, in which it occurs in a wide range of acidic habitats, although usually on mineral soils. He suggested that, while the northern race may have entered Finland from the north and east, the southern race migrated from the south during the Post-Glacial climatic optimum. Although the position with regard to subsp. *strictissima* and subsp. *erecta* in southern Fennoscandia is not yet clear, an examination of herbarium specimens shows that both subspecies occur in Sweden and Norway and in southern Finland, while another race is found in the north. Vasari and I agree (pers. comm.) that his northern race is a new subspecies and is not equivalent to var. *strictissima* as had been earlier suggested. Elsewhere in its range, subsp. *strictissima* seems usually to occur at a greater altitude than subsp. *erecta*.

At present subsp. *strictissima* is only recorded from 14 sites in the British Isles (Table 4). These sites have been traced through an examination of only two herbaria, although perhaps 600 gatherings of *P. erecta* have been examined in all. Many gatherings from upland sites have proved to be subsp. *erecta* and a search in suitable habitats in northern England in August 1971 confirms the suspicion that subsp. *strictissima* is local and apparently absent from many suitable sites. Nevertheless, it is likely that many stations for this subspecies remain undiscovered and that it is widespread, if local, in suitable habitats above 500 m.

In only one case so far in Britain has it been shown that the two subspecies occur together. In nearly all stations there are few problems of identification, the plants being readily identified with one of the two subspecies. However, on Widdybank Fell, Co. Durham, both occur, and some intermediates were noted in the field there by Vasari and myself. Thirteen of these brought into cultivation are maintaining their intermediate status. At this station, communities dominated by *Calluna* occur in juxtaposition with limestone grassland at 500 m. Subsp. *erecta* is confined to the limestone, and subsp. *strictissima* to the *Calluna*-dominated peat, where intermediates are also found, although the latter are commonest in transition zones.

Zimmeter (1884) noted that subsp. *erecta* and subsp. *strictissima* sometimes occur together in central Europe, and Hegi (1922) has recorded intermediates from the same area. Vasari (1968) showed that some populations occurring in the boundary zone between the northern and southern Finnish races are intermediate, and a recent examination of his herbarium material has revealed that all three sorts of intermediate between the northern race (as yet unnamed), subsp. *erecta* and subsp. *strictissima* are occasionally found in Finland. It is likely that, although each of these races originated in isolation, they meet in geographically and ecologically intermediate stations in Finland, and that the resulting hybridisation can give rise to new genetic combinations which are more successful in the intermediate habitats in which they are found, and which are not identifiable with any of the three subspecies. Intermediates do not seem to be very common in Finland, however, and in both Finland and the British Isles they would seem to be sufficiently infrequent to allow the subspecific separation of the races.

We may assume that the subspecies are usually kept separate through environmental pressures. The high-altitude dwarf-shrub communities favoured by subsp. *strictissima* in the British Isles (and in central Europe?) are substantially different from the majority of communities in which subsp. *erecta* is found, and at least some of the characters of the former could be interpreted as being of advantage in the dwarf-shrub community. The stiff, erect, long stems would enable it to compete with the relatively tall *Empetrum* and *Calluna* with which it grows; the larger flowers would enhance their visibility in this tall community; and the long pedicels would similarly aid seed dispersal. However, dwarf-shrub communities are also found at low altitudes, where *P. erecta* is not frequent and in the British Isles occurs only as the subsp. *erecta*. It may be that subsp. *strictissima* maintains a physiological advantage at high altitudes and latitudes, perhaps enabling it to survive low temperatures more readily, and that this adaptation confers a disadvantage in warmer areas, possibly with respect to growth rates. This much is conjecture, but one may assume that subsp. *strictissima* is adapted to colder habitats, being apparently restricted to upland or northern sites.

The wide distribution of subsp. *strictissima* through much of Europe suggests that it may have once inhabited lowland areas from which it is now largely absent (although a relatively low altitude record from Belgium is of interest). It may be an arctic-alpine relic, surviving from the Full-Glacial period. Alternatively, it may have arisen more recently, and have spread in relatively cool conditions, as in the Pre-Boreal or Boreal periods. Whatever the means of origin and spread, it seems likely that subsp. *strictissima* is found in upland and northern areas of Europe as a relic from colder times, only able to survive in conditions resembling the period in which it evolved.

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