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Variation of *Potentilla erecta* (Rosaceae) in Estonia

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Infraspecific variation of Estonian *Potentilla erecta* (L.) Räusch. was studied with different morphometrical methods. Both *P. erecta* ssp. *erecta* and ssp. *strictissima* (Zimm.) A. J. Richards were identified with ssp. *strictissima* prevailing; however, several specimens are morphologically of an intermediate type. Representatives of the two taxa have no geographical or ecological preference in Estonia, and since it was not possible to statistically delimit them, we preferred to treat these taxa as varieties: *P. erecta* var. *erecta* and *P. erecta* var. *strictissima* (Zimm.) Hegi.

Key words: Estonia, infraspecific taxonomy, multivariate methods, *Potentilla erecta*

INTRODUCTION

Potentilla erecta (L.) Räusch. (sect. *Tormentillae* Rydb.) is widespread in Estonia and quite common in Latvia and Lithuania on moderately moist and moist mineral soils and peat (Leht *et al*. 1996). Being a genetically and phenotypically widely variable taxon, it has been treated rather differently: Hegi (1922) has summarized its infraspecific taxonomy and listed 19 taxa of different ranks and taxonomic significance (excluding synonyms) that can be joined under the name *P. erecta.* Also, the multitude of synonyms, more than 30 (Leht 1984), points to its variability.

Variation of *Potentilla erecta* has been thoroughly studied by Vasari (1968) in Finland and by Richards (1973) in Great Britain. They established three different races (subspecies): two in Great Britain and three in Finland (Richards 1973). On the British Isles, the most common is the race growing on lowlands, identified as *P. erecta* ssp. *erecta*. The race of higher altitudes (500 m a.s.l.), *P. erecta* ssp. *strictissima* (Zimm.) A. J. Richards, is rarer. In Finland, *P. erecta* ssp. *strictissima* dominates, and *P. erecta* ssp. *erecta* occurs mostly in the SW part of the country (Richards 1973). The race growing on a thick peat layer in North Finland represents a subspecies which Vasari has not yet described. According to Vasari (1968), the border between the northern race and the other two subspecies coincides roughly with the border between the Southern Boreal and Mid-Boreal vegetation zones (Ahti *et al.* 1964).

According to Richards (1973), *Potentilla erecta* ssp. *strictissima* is found, as a relic from colder climatic periods, in uplands and in northern regions of Europe, where it is able to survive only in conditions resembling those of the period during which it evolved. Vasari (1968) suggests that the northern race is an old constituent of the Finnish flora, while his southern race (*P. erecta* ssp. *erecta* and *P. erecta* ssp. *strictissima* together) is likely to have migrated from the south during the post-glacial climatic optimum.

Since Estonia is the nearest southern neighbouring territory to Finland, it seemed interesting to attempt to confirm Vasari's (1968) approach as well as to find answers to the following questions:

— How variable is *Potentilla erecta* in Estonia?
— Is it possible to identify *P. erecta* ssp. *erecta* and *P. erecta* ssp. *strictissima* on the basis of Estonian material?
— Is it statistically justified to divide *P. erecta* into subtaxa?

MATERIAL AND METHODS

The material studied was mostly collected in 1988 and 1996; and herbarium specimens from the Herbarium of the Institute of Zoology and Botany (TAA), located in Tartu, were also used.

Eighteen macromorphological characters (Table 1) were measured with a binocular microscope MBS-2 or with a ruler. To reduce the effects of individual variability, characters 2–6, 8–11, 13 and 14 were measured three times, and the corresponding average values were used for further calculations. A total of 180 specimens were studied.

The distribution patterns of the subspecies of *Potentilla erecta* in adjacent sites were studied in transitional (mixotrophic) mire and transitional mire-forest habitats in the Alam-Pedja Nature Reserve (Central Estonia) on two transects (300 m and 800 m), where all flowering specimens of *P. erecta*, 60 altogether, were collected. The length of their branches was measured to compare the height of the two subspecies; in cluster analysis this character was not used.

The distribution of the subspecies in Estonia was investigated on the herbarium material of both TAA and the Herbarium of the University of Tartu (TU); over 300 specimens were studied.

The material collected is preserved in TAA.

Data processing

For standardized data, Ward's clustering method with the Manhattan distance as a resemblance measure was employed. Then, using the result as the initial group membership vector, further optimization of classification by k-means procedure was carried out. Ward's clustering was performed by SAS (SAS Institute Inc. 1994), k-means clustering, by SYN-TAX 5.0 program (Podani 1993) packages.

Principal components analysis was used for the ordination of ln-transformed data (CANOCO package, version 3.1; Ter Braak 1990, and CANODRAW package, version 3.0; Smilauer 1992). To calculate means and standard errors as well as to evaluate characters' importance within clusters by ANOVA, the SAS program package was used.

To estimate adjacency of clusters, the distances of all specimens, or operational taxonomic units (OTUs), from all centroids (except for the cluster to which the OTU belongs) were calculated according to the postulate that the j-

Table 1. Morphological characters of measured *Potentilla erecta* (L.) Räusch. specimens.

No.	Notation	Characters
1	NOD	Number of nods under the first branch
2	LFL	Length of the central leaflet (mm)
3	LFW	Width of the central leaflet (mm)
4	TEETH	Number of teeth of the central leaflet
5	STPL	Length of the stipule (mm)
6	STPW	Width of the stipule (mm)
7	FLWS	Number of flowers
8	TOL	Length of the central tooth (mm)
9	TOW	Width of the central tooth (mm)
10	SEPL	Length of the sepal (mm)
11	SEPW	Width of the sepal (mm)
12	BRCH	Number of branches on the shoot
13	LPET	Length of the petal (mm)
14	WPET	Width of the petal (mm)
15	HU	Hairiness of the upper side of the leaflet (1 = glabrous, 2 = hairy)
16	HL	Hairiness of the lower side of the leaflet (1 = glabrous, 2 = hairy)
17	DSTP	Division depth of the stipule (1 = to the base, 2 = 3/4 of the way, 3 = 1/2 of the way, 4 = 1/4 of the way)
18	DLF	Length of the dentated part of the leaflet (1 = to the base, 2 = 3/4 of the way, 3 = 1/2 of the way, 4 = 1/4 of the way)

th cluster is interpreted as adjacent to the i-th cluster if the distance between at least one of the OTUs of the i-th cluster and the centroid of the j-th cluster is shorter than the distance to the centroids of all other clusters (Paal & Kolodyazhnyi 1983, Paal 1994).

In order to measure the degree of distinctness of clusters, the α-criterion (Duda & Hart 1976) was used. To acquire a better interpretation of estimates, it is more convenient to apply the corresponding probabilities as coefficients of indistinctness (I) instead of direct values (Paal 1987, 1994).

The last two analyses were made by the original SYNCONT 3.0 program.

RESULTS

Clusters

Using Richards' (1973) characters, 101 specimens were identified as *Potentilla erecta* ssp. *strictissima* and 45 as *P. erecta* ssp. *erecta*, 34 appeared intermediate.

Potentilla erecta ssp. *strictissima* has larger leaflets with more teeth, larger stipules and more flowers; the dentated part of its leaves is longer, and stipules are divided deeper (the other characters do not reveal any difference (Table 2)). According to ANOVA F-criterion (Table 3), it is these characters that are important in distinguishing the subspecies, with the length of the dentated part of the leaflet and the depth of division of the stipule being the most important ones.

The dendrogram showing the results of the classification by Ward's algorithm (Fig. 1) is split, at a comparatively high level (level I), into two significantly distinct (I = 0.0) clusters, the first (cluster I_1) consisting of 61 and the second (I_2) of 119 specimens. The ratio of ssp. *erecta* to ssp. *strictissima* in the clusters is 1:5 and 1:1.5, respectively.

After reorganizing the obtained classification by k-means procedure, the clusters contain 89 and 91 specimens, and ratios of ssp. *erecta* to ssp. *strictissima* are 1:4 and 1:2, respectively. The coefficient of distinctness of the clusters is in this case also close to zero, despite their partial overlapping in the character space (Fig. 2). The most important characters in determining the clusters at level I are the length of the stipule, the length and width of the leaflet and the length and width of the central tooth (Table 3).

Plants belonging to cluster I_1 have larger leaflets and stipules, their stipules are not deeply divided, their flowers are larger and more numerous. Plants in cluster I_2 are smaller, and have more

Table 2. Mean ± SE of the characters of *Potentilla erecta* (L.) Räusch. ssp. *erecta* and *P. erecta* ssp. *strictissima* (Zimm.) A. J. Richards and two clusters obtained by k-means. Denotation of characters as in Table 1.

Character	Conventional estimation		Clustering by k-means algorithm	
	ssp. *erecta* n = 45	ssp. *strictissima* n = 101	Cluster I_1 n = 89	Cluster I_2 n = 90
NOD	2.42 ± 0.20	2.19 ± 0.16	2.07 ± 0.12	2.43 ± 0.17
LFL	21.24 ± 0.68	24.23 ± 0.65	27.11 ± 0.62	19.94 ± 0.37
LFW	7.24 ± 0.32	7.56 ± 0.20	8.86 ± 0.22	6.42 ± 0.15
TEETH	8.60 ± 0.30	10.27 ± 0.88	10.97 ± 1.00	8.36 ± 0.17
STPL	11.36 ± 0.40	12.69 ± 0.35	14.56 ± 0.32	10.28 ± 0.21
STPW	8.42 ± 0.42	9.69 ± 0.34	11.23 ± 0.37	7.63 ± 0.20
FLWS	8.87 ± 0.97	11.26 ± 0.94	11.67 ± 1.01	9.16 ± 0.72
TOL	2.46 ± 0.09	2.61 ± 0.08	2.74 ± 0.09	2.39 ± 0.07
TOW	1.25 ± 0.06	1.21 ± 0.03	1.32 ± 0.03	1.14 ± 0.03
SEPL	2.96 ± 0.06	3.18 ± 0.05	3.32 ± 0.05	2.93 ± 0.05
SEPW	1.47 ± 0.03	1.47 ± 0.02	1.59 ± 0.02	1.37 ± 0.02
BRCH	1.98 ± 0.02	1.97 ± 0.07	1.93 ± 0.04	1.98 ± 0.07
LPET	3.83 ± 0.11	3.70 ± 0.08	4.03 ± 0.08	3.52 ± 0.07
WPET	3.49 ± 0.13	3.40 ± 0.08	3.69 ± 0.09	3.24 ± 0.08
HU	2.00 ± 0.00	1.95 ± 0.02	1.96 ± 0.02	1.98 ± 0.02
HL	1.98 ± 0.02	1.98 ± 0.01	1.99 ± 0.01	1.97 ± 0.02
DSTP	2.71 ± 0.11	2.38 ± 0.08	2.60 ± 0.08	2.31 ± 0.08
DLF	2.62 ± 0.10	2.48 ± 0.06	2.53 ± 0.08	2.56 ± 0.06

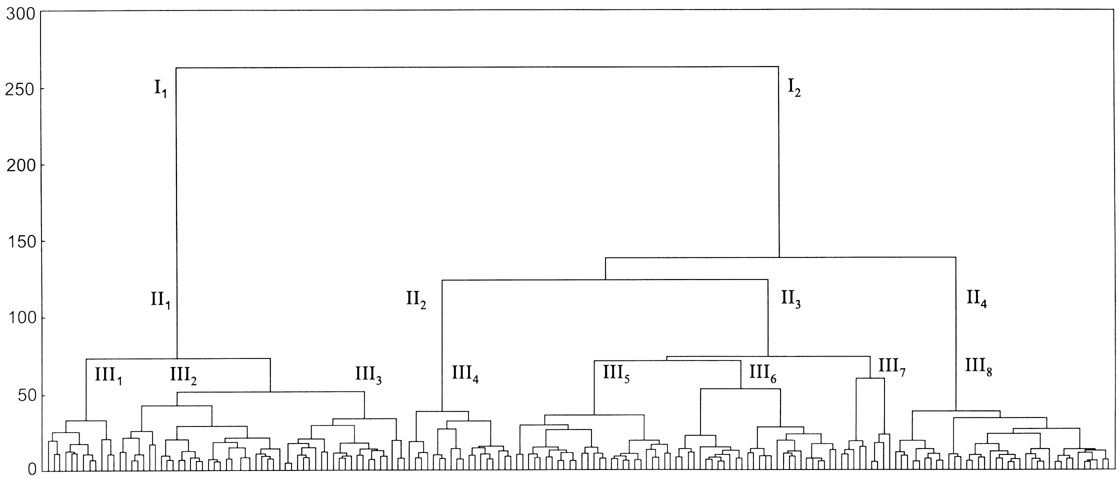

Fig. 1. Dendrogram of clustering *Potentilla erecta* (L.) Räusch. specimens according to Ward's algorithm, Manhattan distance.

nods. No difference is observed in the branching of plants, in the hairiness of leaflets or in the length of the dentated part of the leaflet.

In the dendrogram (Fig. 1) cluster I_2 is clearly divided at the level of the linkage distance of 120–140 units (level II), into three smaller clusters (II_2, II_3, II_4), whereas cluster I_1 remained unsplit at this level. Two cluster pairs have the coefficients of indistinctness higher than 5% ($I_{II_2,II_3} = 46.9$, $I_{II_2,II_4} = 8.0\%$) and are thus insignificantly separated. After reorganizing the clusters by k-means procedure, their size remains nearly the same, and

Table 3. Importance of morphological characters (C) of *Potentilla erecta* (L.) Räusch. in delimiting infraspecies-clusters according to ANOVA *F*-criterion (*F*). Denotation of characters as in Table 1. Subspecies = specimens with intermediate characters excluded; KM-2 = clusters obtained by k-means procedure at the two-cluster level; KM-4 = clusters obtained by k-means procedure at the four-cluster level; KM-8 = clusters obtained by k-means procedure at the eight-cluster level.

Subspecies		KM-2		KM-4		KM-8	
C	*F*	C	*F*	C	*F*	C	*F*
LFL	8.08	STPL	134.43	STPL	126.36	STPL	173.19
DSTP	6.04	LFL	117.04	LFL	84.41	LFL	121.01
SEPL	4.85	LFW	64.16	STPW	83.32	TOW	102.36
STPL	4.58	STPW	59.51	LFW	56.35	STPW	75.93
STPW	3.69	SEPW	43.04	TOW	51.74	LFW	67.54
TEETH	3.29	SEPL	33.62	TOL	30.22	TOL	62.23
FLWS	2.62	LPET	22.28	TEETH	12.76	TEETH	15.63
HU	2.31	TOW	15.63	FLWS	5.70	DLF	6.38
DLF	1.49	TEETH	15.51	DLF	5.15	FLWS	4.81
LPET	1.11	WPET	14.22	SEPL	1.77	HL	3.78
NOD	0.91	TOL	10.00	SEPW	1.41	HU	2.18
TOL	0.84	DSTP	6.57	NOD	1.40	LPET	1.10
LFW	0.73	FLWS	4.31	LPET	1.19	SEPL	1.03
BRCH	0.32	NOD	2.78	HL	0.95	SEPW	0.83
WPET	0.22	HL	0.99	BRCH	0.88	BRCH	0.82
TOW	0.17	HU	0.71	HU	0.71	DSTP	0.57
SEPW	0.01	DLF	0.20	WPET	0.28	WPET	0.50
HL	0.01	BRCH	0.04	DSTP	0.10	NOD	0.00

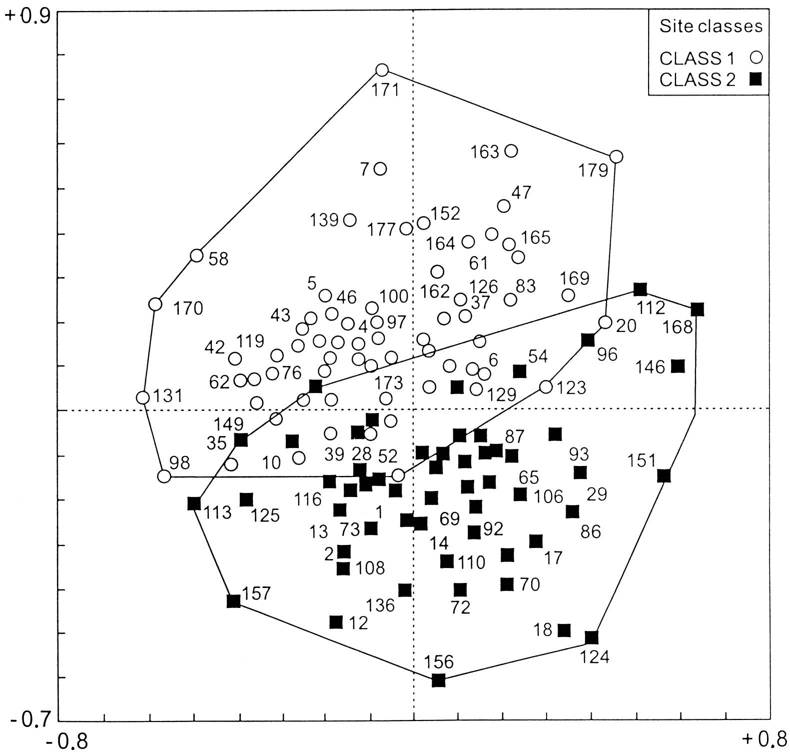

Fig. 2. Classification polygons superimposed onto a PCA scatterplot. Clusters obtained at the two-cluster level by k-means procedure.

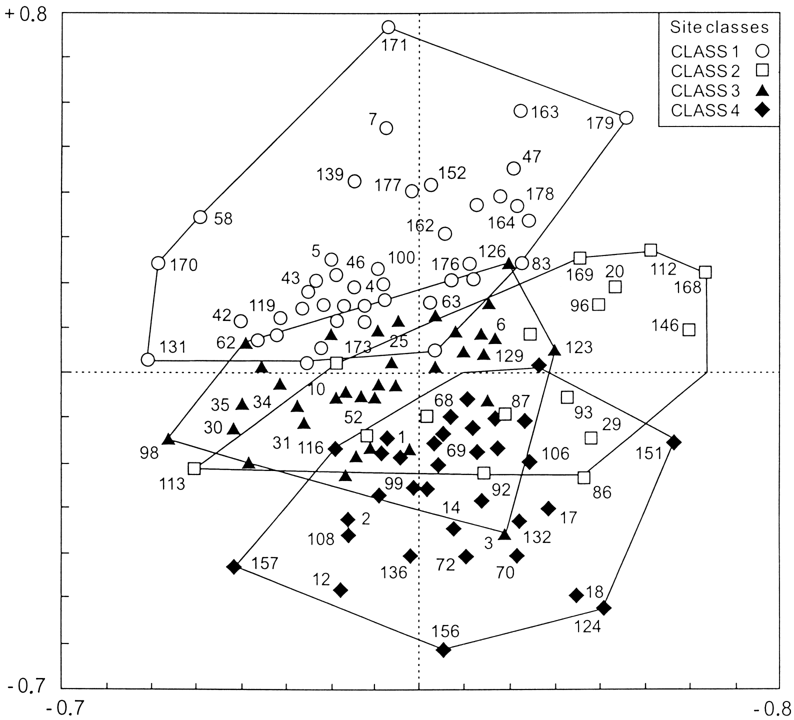

Fig. 3. Classification polygons superimposed onto a PCA scatterplot. Clusters obtained at the four-cluster level by k-means procedure.

the same cluster pairs are indistinct (Fig. 3); however, the coefficients of indistinctness are now lower, $I_{\mathrm{II}_2,\mathrm{II}_3} = 20\%$ and $I_{\mathrm{II}_2,\mathrm{II}_4} = 5.5\%$, respectively. None of the clusters contain representatives of only one of the putative subspecies: the ratios of ssp. *erecta* to ssp. *strictissima* are 1:4, 1:2.5, 1:2 and 1:1.

The characters that are important for the separation of specimens at level II are mostly the same as at level I, except that the length and width of the central tooth are now much more important than the length and width of the sepal (Table 3). The division depth of the stipule appears unimportant, whereas the length of the dentated part of the leaflet matters to some extent.

In the dendrogram (Fig. 1), clusters II_1 and II_3 are both divided further into 3 pronounced subclusters, which yields 8 clusters in all (III_1–III_8). After using k-means procedure, most cluster pairs (except III_3 and III_7, III_5 and III_7, III_6 and III_7) become distinct. Nevertheless, all clusters are mixed, consisting of both subspecies and intermediates; only cluster III_8 consists predominantly of ssp. *erecta*.

The characters that are most important for distinguishing clusters at level III are the same as those involved in the case of four clusters (level II), whereas their order is somewhat different (Table 3).

Clusters III_1–III_7 differ mostly in metric characters, while the length of the dentated part of the leaflet and the division depth of the stipule do not reveal any clear pattern here. Cluster III_8 (44 specimens) in which *Potentilla erecta* ssp. *erecta* prevails consists of plants with small leaflets, few teeth, small stipules and few nods (1.85 ± 0.2). Their leaves are dentated 1/4–3/4 of the way and the stipules about 3/4 of the way. Cluster III_8 is adjacent to three clusters (III_4, III_5, III_6) which contain relatively more ssp. *erecta* specimens (ratios 1:2, 1:2.5, 1:3). At the same time, this cluster is convincingly separated from clusters where ssp. *strictissima* prevails: it is distinct from these clusters without any adjacency to them.

The second largest cluster (III_3, 25 specimens) consists predominantly of ssp. *strictissima* (ratio 1:11) but is adjacent to clusters III_5 and III_7 and indistinct from cluster III_7, which all contain relatively more specimens of ssp. *erecta*. Therefore, it is quite complicated to delimit ssp. *erecta* and *strictissima* even at the level of comparatively small clusters; the only different group seems to be cluster III_8 which corresponds more or less also to cluster II_4.

Characters

Correlation between the characters is not very strong; Spearman's rank correlation coefficients exceeding the arbitrary level of 0.60 occurred only between the length and width of the leaflet (0.74), between the length of the leaflet and length of the stipule (0.85), between the length of the leaflet and width of the stipule (0.62), between the length of the stipule and width of the leaflet (0.70), and between the length and width of the central tooth (0.73). This can also be observed on the character vector plot (Fig. 4) where the above characters form a compact bunch of vectors. The opposite positions on the ordination plot are occupied by the number of flowers and branches, and the number of nods. In case of more strongly correlated characters, the length of their vectors on the plot corresponds well to their importance in distinguishing clusters according to the *F*-criterion (Table 3).

It is remarkable, however, that the length of the dentated part of the leaflet and the division depth of the stipule, which were considered by Richards important characters for delimiting ssp. *erecta* and ssp. *strictissima*, are rather weakly correlated ($r = 0.23$). According to the diagnosis, plants of ssp. *strictissima* must have stipules divided nearly to the base and leaflets dentated nearly to the base; in ssp. *erecta* stipules are divided less than half way and leaflets dentated only in the upper part.

Habitat preferences

When considering habitat preferences of plants in different clusters, either on mineral soil or peat, no correlations were found; all clusters contained plants from both habitats.

Among the studied herbarium specimens of TAA and in TU, ssp. *strictissima* was more common; several intermediates were also found. The plants of the two subspecies and their intermediates had been growing on a large variety of soils from gley–podzols and gley soils to peaty and peat soils.

Sixteen out of the 60 plants collected to estimate the distribution of subspecies in adjacent localities were identified as ssp. *erecta*, 25 as ssp.

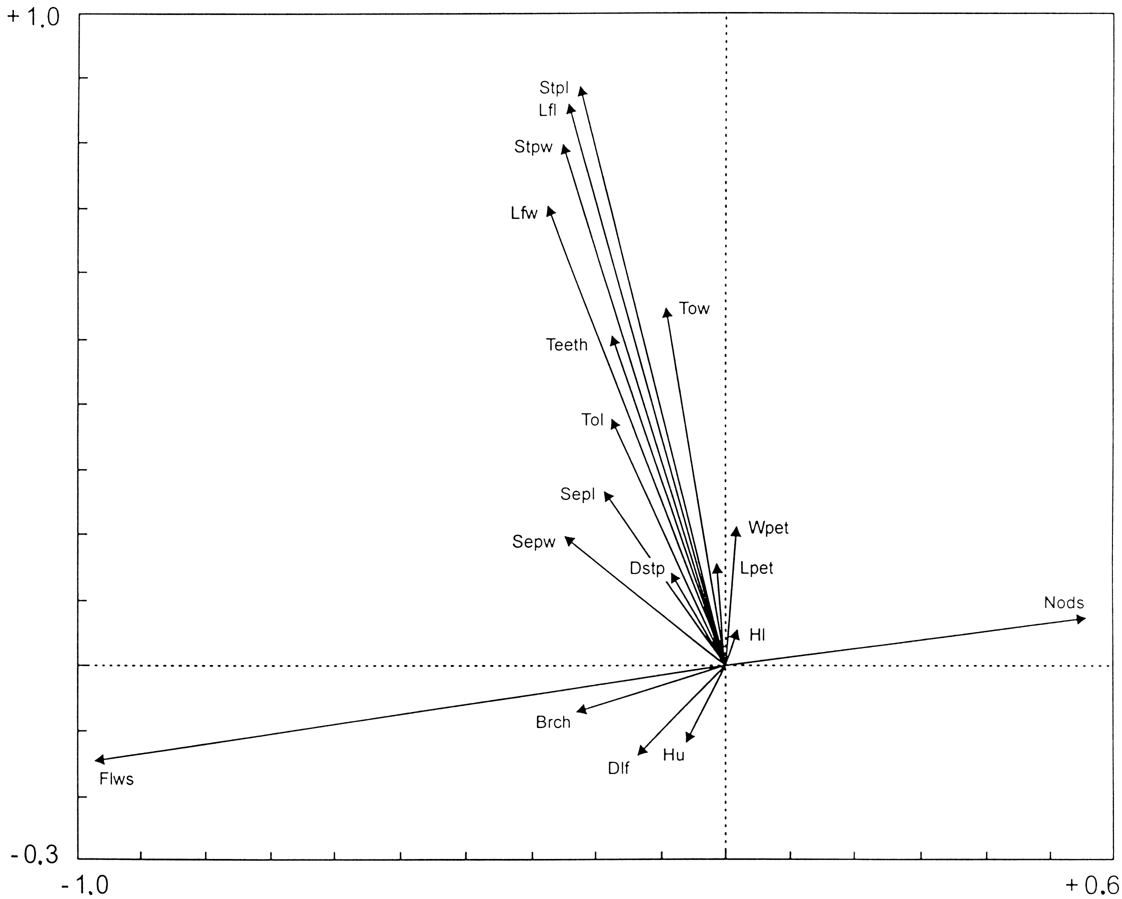

Fig. 4. PCA ordination of morphometrical characters of *Potentilla erecta* (L.) Räusch. specimens. Abbreviations as in Table 1.

strictissima and 19 appeared to be intermediates. Hence, no differences could be seen in the distribution of subspecies on peaty soil.

The height of *Potentilla erecta* ssp. *erecta* specimens collected from transects was 20–65 cm and that of ssp. *strictissima*, 30–80 cm.

DISCUSSION

Vasari (1968) did not consider the dentation of leaflets and stipules, i.e. the characters used by Richards (1973), and found it possible to separate the two subspecies in his southern race only after discussion with Richards (Richards 1973). In the Estonian material these characters occurred quite often in an unexpected way: stipules were divided nearly to the base and leaflets were dentated only in the upper 1/4 or 1/2, or vice versa.

The division depth of the stipule (DSTP) and the length of the dentated part of the leaflet (DLF) were weakly correlated ($r = 0.23$), and only the division depth of the stipule was important in distinguishing subspecies (Table 3). When clustering the material into four or eight clusters, DSTP had almost no importance at all, DLF being slightly more important. In the case of two clusters, DSTP and DLF had swapped positions (Table 3). Therefore, these characters do not seem to be discriminative enough in the nordic material but are more useful in the case of material from other parts of the areal.

According to Richards (1973), *Potentilla erecta* ssp. *erecta* has more and larger flowers than ssp. *strictissima*, the teeth of its leaflets should not exceed 1.5 mm and the leaflets 20 mm in length and the length of its stems should be up to 150 mm.

Considering the Estonian material, it seems that *Potentilla erecta* ssp. *erecta* does not meet these criteria in all respects. Our plants tended to be taller (e.g. on transects in Alam-Pedja the branch length of ssp. *erecta* specimens was 20–65 cm, that of ssp. *strictissima* 30–80 cm), and the difference in the size of flowers, if any, was very slight. Leaflets and their teeth were often larger, and it was ssp. *strictissima* that tended to have more flowers than ssp. *erecta* (Table 2). When analysis was based only on specimens identified as ssp. *strictissima* and ssp. *erecta,* the most important characters for distinguishing the taxa appeared to be the length of the leaflet, length of the sepal, length and width of the stipule, and the number of teeth and flowers (Table 3). When, however, intermediates were included, the corresponding *F*-criterion value of all characters was very low, indicating that the separation power of the characters was low too, which makes discrimination between the groups very difficult.

The two subspecies have been observed to occur together in only one locality on the British Isles where a few intermediates have also been found (Richards 1973). Zimmeter (1884) noted that ssp. *erecta* and ssp. *strictissima* sometimes occur together in Central Europe, and Hegi (1922) has recorded intermediates from the same area. In Finland, intermediates between all the three subspecies occasionally occur. Richards (1973) suggests that although each of these races originated in isolation, they meet in geographically and ecologically intermediate localities in Finland.

Since Estonia is a low-lying country (maximum elevation 318 m), ssp. *strictissima* grows here in habitats different from those it favours on the British Isles and in Central Europe. *Potentilla erecta* ssp. *strictissima* and ssp. *erecta* have no ecological or geographical preference in Estonia: they both grow on various soils, in rather wet places and in moderately moist habitats. Intermediates can be found everywhere.

TAXONOMIC CONCLUSIONS

In Estonia, both *Potentilla erecta* ssp. *erecta* and ssp. *strictissima* occur, ssp. *strictissima* being more common. Therefore, the theory of their migration from the south to Finland (Vasari 1968) seems to be plausible.

Often *Potentilla erecta* ssp. *erecta* and ssp. *strictissima* grow together, and their intermediates seem to be common. However, it was not possible to delimit the two subspecies even at the level of small clusters; all the clusters obtained were mixed ones.

Already Wolf (1908), when characterizing his varieties of *Potentilla erecta* (he recorded six), mentioned that four of them (incl. var. *strictissima* and var. *typica*) are sometimes difficult to distinguish and that intermediate forms exist.

According to our material, these taxa are much more variable and transitional in Estonia than on the British Isles. Hence, they are not worthy of the rank of the subspecies but should rather be referred to as varieties, since the rank of the subspecies (race) is used for taxa that have their own geographical areal and/or established ecological preference.

As the material appeared to be morphologically quite varying and the clusters obtained distinct, the infraspecific taxonomy of the species needs further investigation over a more extensive area of distribution with the use of more elaborated methods (DNA and/or isozyme analysis etc.).

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