Variation of *Potentilla* sect. *Potentilla* (Rosaceae) in Estonia and neighbouring countries

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One-hundred and eighty specimens of *Potentilla erecta*, 58 of *P. reptans*, 49 of *P. anglica* and 19 of *P.* × *italica* were studied phenetically using 19 macromorphological characters. As *P. erecta* and *P. reptans* are quite common in Estonia, while *P. anglica* is absent from that country, the occurrence of *P.* × *italica* in Estonia points to its possible origin from hybridization of the former two species. Estonian *P.* × *italica* produces no seeds and is hexaploid (2n = 42). *Potentilla* × *italica* and *P. anglica* appeared, from the statistical point of view, morphologically well separable from each other as well as from their putative parents. In comparison with the varieties of *P. erecta*, var. *erecta* and var. *strictissima*, which do not cluster into separate groups, it is reasonable to treat *P.* × *italica*, which clearly forms clusters of its own, on the same level as *P. reptans* and *P. anglica*, i.e., to recognize it as a morphologically stable nothospecies.

Keywords: *Potentilla anglica*, *Potentilla erecta*, *Potentilla* × *italica*, *Potentilla reptans*, phenetics, taxonomy

Introduction

The group *Tormentillae* (sect. *Potentilla*), as described by Wolf (1908), comprises eight species and some hybrid taxa, of which *Potentilla reptans*, *P. erecta*, *P. anglica*, and one of their hybrids, *P.* × *italica* are found in the Baltic states. These three species are related so that *P. anglica* is an allo-octoploid (2n = 56) originating from the hybridization of *P. erecta* (2n = 28) and *P. reptans* (2n = 28) (Matfield & Ellis 1972, Ietswaart & Kliphuis 1985). Hybrids of *P.*

anglica × *P. erecta* (*P.* × *suberecta*), *P. erecta* × *P. reptans* (*P.* × *italica*) and *P. anglica* × *P. reptans* (*P.* × *mixta*) have been found in the nature (Ball *et al.* 1968, Ietswaart & Kliphuis 1985), and they have also been produced experimentally (Czapik 1968, Matfield *et al.* 1970, Matfield 1972, Matfield & Ellis 1972).

Experimental hybridizations have shown that hybrids very similar to *Potentilla* × *mixta* can be produced in two ways: either by occasional successful pollination of *P. reptans* by *P. anglica*, or by hybridization between autopolyploid *P.*

reptans and tetraploid *P. erecta*. Thus, it is possible that natural hexaploid hybrids include plants whose origin is different, but which are morphologically and cytologically indistinguishable (Matfield *et al.* 1970, Czapik 1975, Matfield & Walters 1975). In floral lists even the name *P. × mixta s. lato* with an explanation (*P. erecta* or *P. anglica × P. reptans*) is used (Staffordshire Biodiversity Action Plan 2001, Flora of Northern Ireland 2000–2001). We refer to *P. erecta × P. reptans* as *P. × italica*.

A typical *Potentilla × mixta* has 42 chromosomes as does also *P. × italica*; they both are often sterile but reproduce abundantly by runners. In their genetic constitution, four genomes of *P. reptans* and two genomes of *P. erecta* are involved; therefore, in many characters of *P. × mixta s. lato*, domination of *P. reptans* is recognizable (Matfield *et al.* 1970, Czapik 1975). An extremely poor seed set combined with highly effective vegetative reproduction classifies *P. × mixta* and *P. × italica* as vegetative apomicts (Czapik 1975).

Potentilla erecta is very common in Estonia and quite common in Latvia and Lithuania on moderately moist to moist mineral soils and on peat. *Potentilla reptans* thrives in meadows and wooded meadows, on grasslands, seashores, roadsides and in other open habitats in the western regions of Estonia as well as in all parts of Latvia and Lithuania (Leht *et al.* 1996). *Potentilla anglica* is absent from Estonia and Lithuania and is known only from one locality in Latvia near Riga on a sandy pine forest edge, where it was refound in 1988 after a one-hundred-year interval (Leht 1989). In 1997 several specimens among Estonian herbarium material, dated from the 1930s and 1940s, were identified as *P. × italica*. They all originated from neighbouring localities on the shores of Lake Võrtsjärv. However, in 1997, *P. × italica* plants were found in only one of these localities, while the other sites were overgrown with shrubs.

Phenotypically, *Potentilla erecta* is a variable taxon, which has been dealt with in various ways: Hegi (1923) cited 19 taxa of different ranks and various taxonomic significance that can be joined under the name *P. erecta*. Its variation in Estonia was studied by Leht and Paal (1998b) and will not be discussed in detail in the current paper.

Morphological variation is said to be comparatively limited in *Potentilla reptans*, moderate in *P. anglica*, and fairly large in the hybrids

Table 1. Morphological characters used in analysis. Characters 7–19 were measured in triplicate and average values used for calculations. Characters 7–13, 16, and 17 were measured on successive cauline leaves in the central part of the shoot.

No.	Denotation	Character
1	NOD	Number of nodes under the first branch
2	BRCH	Number of branches on the shoot
3	HU	Hairiness of the upper side of the leaflet (1 = glabrous, 2 = sparsely hairy, 3 = densely hairy)
4	HL	Hairiness of the lower side of the leaflet (1 = glabrous, 2 = sparsely hairy, 3 = densely hairy)
5	RL	Rosette leaves (1 = over 5, 2 = up to 5, 3 = absent)
6	FLWS	Number of flowers
7	LFL	Length of the central leaflet (mm)
8	LFW	Width of the central leaflet (mm)
9	TEETH	Number of teeth of the central leaflet
10	STPL	Length of the stipule (mm)
11	STPW	Width of the stipule (mm)
12	TOL	Length of the central tooth of the central leaflet (mm)
13	TOW	Width of the central tooth of the central leaflet (mm)
14	SEPL	Length of the sepal (mm)
15	SEPW	Width of the sepal (mm)
16	LFN	Leaflet number
17	PETIOL	Length of the petiole (mm)
18	LPET	Length of the petal (mm)
19	WPET	Width of the petal (mm)

of these species (Ietswaart & Kliphuis 1985). During the cultivation of *P.* × *mixta*, Czapik (1968) noted that it showed remarkable constancy only in respect of its sterility, while the other characters varied largely, which is probably one of the reasons why *P.* × *italica* and *P.* × *mixta* are often overlooked in the nature.

The questions that we address in our study are:

1. How variable phenetically are *P. reptans*, *P. anglica*, and *P.* × *italica*?
2. What is the chromosome number of Estonian *P.* × *italica*?
3. Is *P.* × *italica* a morphologically stable taxon?

Material and methods

A total of 180 specimens of *Potentilla erecta*, 58 of *P. reptans*, 49 of *P. anglica* and 19 of *P.* × *italica* were studied phenetically using 19 macromorphological characters (Table 1). The Estonian material of *P. erecta* and *P. reptans* analysed was mostly collected in 1988 and 1996; herbarium specimens from the Herbarium of the Institute of Zoology and Botany (TAA) were also used. The Finnish and Swedish material of *P. anglica* originates from the Herbarium of the Botanical Museum of the Finnish Museum of Natural History (H). The Estonian material of *P.* × *italica* was collected in 1997; herbarium specimens from TAA were used as well, and four specimens were obtained from Prof. R. Czapik from Kraków (KRA). The material collected from Estonia is preserved in TAA.

The characters (Table 1) were measured on air dried herbarium material using a binocular microscope MBS-2 or a ruler. To reduce the effects of individual variability, characters 7–15, 18 and 19 were measured in triplicate, and the corresponding average values were used in further calculations. Characters 7–13 were measured on successive cauline leaves in the central part of the stem.

Among the material of *Potentilla erecta*, using Richards's (1973) descriptions, 101 specimens were identified as *P. erecta* var. s*trictissima* and 45 as *P. erecta* var. *erecta*; 34 specimens appeared intermediate (Leht & Paal 1998b). In the current study, two of Richards's characters used for identification, division depth of the stipule and length of the dentate part of the leaflet, were not included, as they do not vary in *P. reptans*, *P.* × *italica* and *P. anglica*.

Chromosomes

Chromosomes were counted from root tips taken from young shoots of *Potentilla* × *italica* which started to root in water. Root tips were pretreated with 8-hydroxyquinoline for three hours for accumulation of metaphases, then hydrolysed and stained with concentrated HCl and 1% aceto-orcein (1:9) for two hours or longer at room temperature, and squashed in 45% acetic acid.

The material for chromosome counts was collected in 2001.

Data processing

Clustering of the standardized data was carried out with the program package SYN-TAX 2000 (Podani 2001). The method of the minimal incremental sum of squares, or Ward's method (Podani 2000), with the Manhattan-metric as the proximity measure was employed.

For evaluation of the clusters' distinctness, the probability of the α-criterion (Duda & Hart 1976), termed the coefficient of indistinctness (CI; Paal 1987), was used as in Leht and Paal (1998a, 1998c). In addition, for elucidating mutual relationships between the clusters and the main directions of their variation in the multivariate character space, the adjacency matrix was calculated. Adjacency was expressed as the percentage of specimens in the considered cluster for which the centroid of the cluster to be compared is the closest in the character space (Paal & Kolodyazhnyi 1983).

Discriminant analysis of the STATISTICA package (StaSoft Inc.) was used to determine the set of variables yielding the best discrimination between the species and the established clusters. Canonical discriminant analysis was carried out to produce a scatterplot for the first two discriminant functions (canonical roots).

Results

Morphological variation

All four conventionally established species-clusters are mutually highly distinct (CI = 0.0) from the statistical point of view. The within-group variation of *Potentilla erecta* and *P. reptans* specimens is directed towards *P. anglica* and *P. × italica* clusters, while for 79.6% of the *P. anglica* specimens, the centroid of the *P. erecta* cluster appears to be the closest (Table 2). Of the *P. × italica* specimens, 52.6% show certain affinity with the cluster of *P. reptans*; to a lesser extent, their variation is directed also towards the centroids of *P. erecta* and *P. anglica*.

On the scatterplot of the canonical roots, where grouping was established according to the species-clusters (Fig. 1), the specimens of *Potentilla erecta* form a well-separated and compact group. The clusters of *P. anglica* and *P. reptans* are more diffuse and partly overlapping with the cluster of *P. × italica* located between them. Due to reduced dimensions, the scatterplot does not reflect the relationships between the clusters as explicitly as does Table 1. Yet the mutually directed variation of the clusters of *P. erecta* and *P. anglica* is quite obvious, while variation of *P. reptans* specimens is directed mainly towards the *P. × italica* cluster.

The dendrogram showing the results of cluster analysis (Fig. 2) is clearly split into two clusters on the highest level, the first (I_1) comprising *Potentilla erecta* and the second (I_2) consisting of specimens of *P. reptans*, *P. anglica*, and *P. × italica*. Both clusters are further divided again into two large clusters. In clusters II_1 and II_2, specimens of *P. erecta* var. *erecta* and *P. erecta* var. *strictissima* stand intermixed both with each other and with intermediate specimens (speci-

mens that were not identified as var. *erecta* or var. *strictissima*, *see* Leht & Paal 1998b). Cluster II_3 comprises *P. reptans* and three specimens of *P. × italica*; cluster II_4 includes specimens of *P. anglica* and *P. × italica*.

On lower dissimilarity levels, within rather short distances, the phenogram can be split into nine (level III) and finally into 15 subclusters (level IV). When divided into subclusters of level III, the clusters of *Potentilla erecta* (III_1–III_5) remain mixed clusters consisting of specimens of var. *erecta* and var. *strictissima*, as is also the case with subclusters formed on level IV.

The cluster comprising specimens of *Potentilla reptans* (II_3) is divided into two subclusters (III_6 and III_7), while cluster III_6 also includes three specimens of *P. × italica*. Cluster II_4 is split into subcluster III_8, joining exclusively specimens of *P. anglica* and subcluster III_9, comprising only *P. × italica*. All nine subclusters established on level III are reliably distinct, as their coefficients of indistinctness are close to zero in all cases. The material of *P. anglica* collected from Finland and the material originating from Sweden belong mostly to separate subclusters on level IV. But since the subclusters of level IV are small and usually indistinct, only the subclusters of level III will be further analysed.

The subclusters of *Potentilla erecta* are mostly adjacent to each other in the character space, except for subcluster III_2 where for 32.4% of specimens the nearest neighbour is the centroid of *P. anglica* (III_8) (Table 3). Two other subclusters of *P. erecta* are varying to some extent towards *P. italica*: the centroid of subcluster III_9 is the most adjacent for 13.3% of the specimens of subcluster III_4 and for 6.7% of the specimens of subcluster III_5.

The within-group variation of the first *Potentilla reptans* subcluster (III_6) is directed mainly towards *P. anglica* (III_8, 66.7%) and *P. × italica* (III_9, 20.4%), while the other subcluster of *P. reptans* (III_7) is the nearest neighbour for only 13.0% of the specimens. For all specimens of the smaller subcluster of *P. reptans* (III_7), the closest neighbour is the centroid of *P. × italica* (III_9). Specimens of *P. anglica* (III_8) recognise two subclusters of *P. erecta* as the most adjacent (III_1, 22.5% and III_2, 71.4%). The subcluster of *P. × italica* (III_9) varies in many directions; varia-

Table 2. Adjacency matrix of conventionally estimated species-clusters.

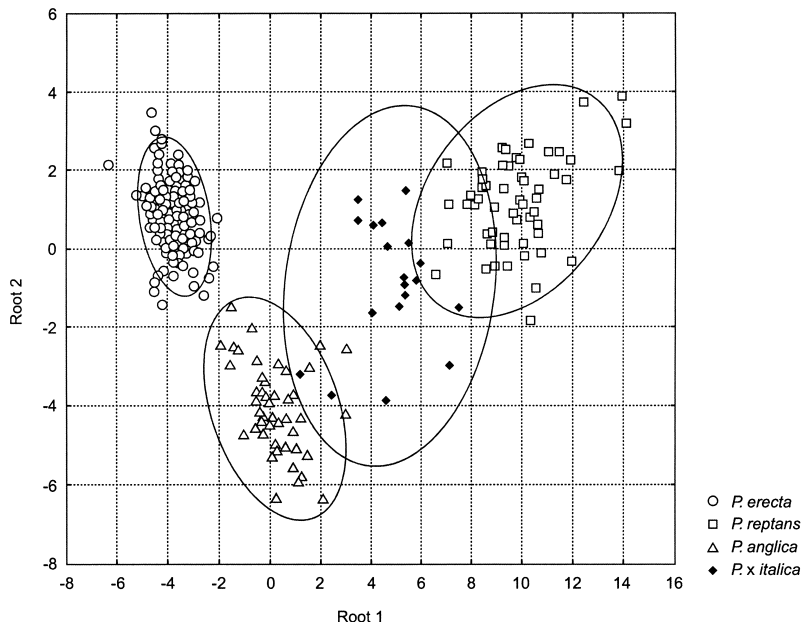| Cluster analysed	Cluster compared			
	P. erecta	*P. reptans*	*P. anglica*	*P. × italica*
P. erecta	×	–	56.7	42.8
P. reptans	–	×	43.1	56.9
P. anglica	79.6	16.3	×	–
P. × italica	31.6	52.6	15.8	×

Fig. 1. Scatterplot of specimens by two first canonical roots (axes). Groups correspond to the conventionally established species; ellipses represent the prediction interval of the respective clusters in which a single new observation can be expected to fall with 95% probability.
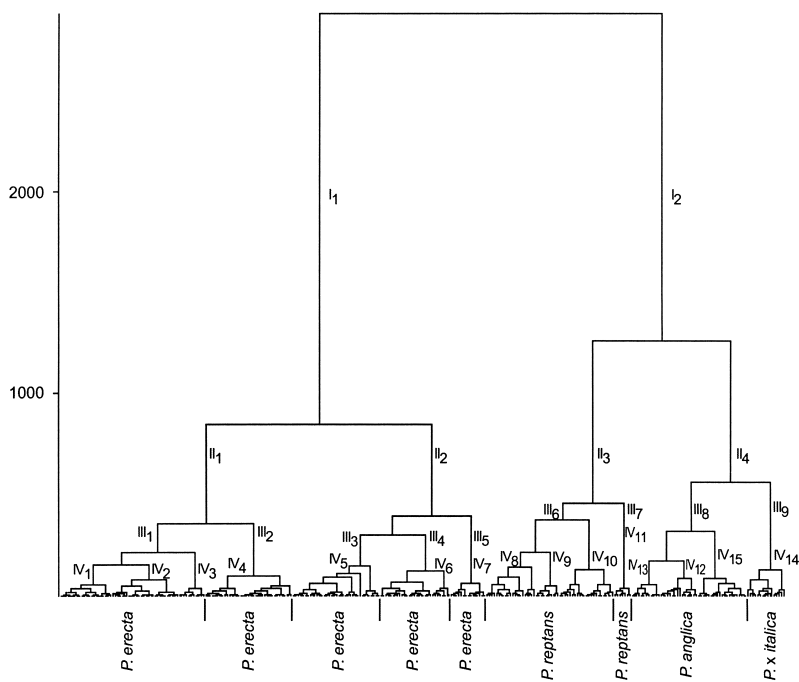

Fig. 2. Phenogram of clustering of standardized morphometric data of *Potentilla erecta*, *P. reptans*, *P. × italica* and *P. anglica* specimens according to the minimal incremental sum of squares algorithm and Manhattan-metric.

tion is more pronounced towards the subclusters of *P. reptans* (III$_6$, 25.0% and III$_7$, 43.8%), and to a lesser extent also towards four subclusters of *P. erecta* (Table 2).

The scatterplot of canonical roots of nine subclusters (Fig. 3) is in a good concordance

with the scatterplot of species (Fig. 1) as well as with the adjacency matrix of the subclusters (Table 3). The first four subclusters of *Potentilla erecta* form an almost totally overlapping cloud, only the specimens of subcluster III$_5$ reveal a wider variation and some overlapping with the
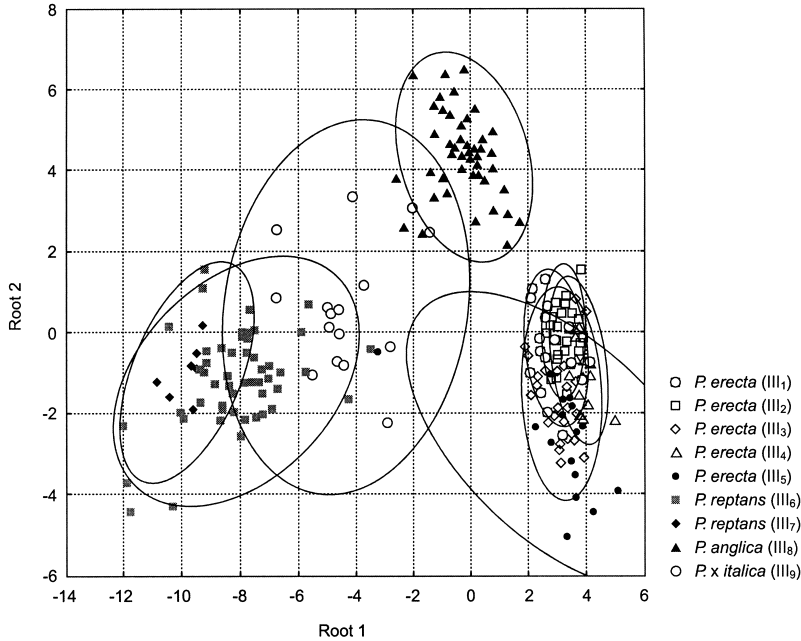
Fig. 3. Scatterplot of specimens by two first canonical roots (axes); groups correspond to the clusters of level III on the phenogram.

Legend:
- ○ *P. erecta* (III$_1$)
- □ *P. erecta* (III$_2$)
- ◇ *P. erecta* (III$_3$)
- △ *P. erecta* (III$_4$)
- ● *P. erecta* (III$_5$)
- ▦ *P. reptans* (III$_6$)
- ◆ *P. reptans* (III$_7$)
- ▲ *P. anglica* (III$_8$)
- ○ *P.* x *italica* (III$_9$)

cluster of *P.* × *italica*. A very large overlapping is also characteristic of the subclusters of *P. reptans* (III$_6$ and III$_7$). The cluster including *P.* × *italica* specimens has again a transitional position between all other subclusters.

Characters

The means of the characters of phenotypically similar *Potentilla reptans*, *P. anglica* and *P.* × *italica* appeared according to multivariate ANOVA analysis all significantly different (Table 4).

In distinguishing conventionally identified species, the most important character is number of leaflets followed by number of rosette leaves, length of the sepal, width of the stipule and width of the central tooth.

The characters important in separation of the subclusters of level III are not exactly the same as in discrimination of the species; now the most important character, number of leaflets, is followed by number of flowers and length of the petiole, slightly less important are the number of rosette leaves and width of the sepal.

Table 3. Adjacency matrix of level III clusters in Fig. 2.

Cluster analysed	Cluster compared								
	III$_1$	III$_2$	III$_3$	III$_4$	III$_5$	III$_6$	III$_7$	III$_8$	III$_9$
III$_1$	×	51.7	43.3	–	–	–	–	–	–
III$_2$	67.6	×	–	–	–	–	–	32.4	–
III$_3$	73.0	–	×	8.1	16.2	–	–	–	–
III$_4$	30.0	–	56.7	×	–	–	–	–	13.3
III$_5$	–	–	86.7	6.7	×	–	–	–	6.7
III$_6$	–	–	–	–	–	×	13.0	66.7	20.4
III$_7$	–	–	–	–	–	–	×	–	100.0
III$_8$	22.5	71.4	–	–	–	–	–	×	–
III$_9$	6.3	–	12.5	6.3	6.3	25.0	43.8	–	×

Chromosomes

The chromosome number counted for *P.* × *italica* was 2n = 42.

Discussion

As *Potentilla erecta* and *P. reptans* are quite common in Estonia, while *P. anglica* is absent, the occurrence of *P.* × *italica* here points to its possible origin from the hybridization between *P. erecta* and *P. reptans*. The relatedness of these species is also confirmed by the evident phenotypical variation of the specimens of *P.* × *italica* towards *P. reptans* and *P. erecta* (Table 2), while much less in the direction of *P. anglica*. However, a certain morphological resemblance of *P.* × *italica* with *P. anglica* can be concluded from the fact that on the phenogram *P.* × *italica* and *P. anglica* belong on the second level of the same cluster (II$_4$).

According to Czapik (1975), *Potentilla* × *italica* has four genomes of *P. reptans* and two genomes of *P. erecta*, which could explain the stronger association between *P.* × *italica* and *P. reptans* compared with its other parent. *P.* × *italica* produces no seeds in Estonia and reproduction takes place only vegetatively by runners. As *P. erecta* and *P. reptans* were not found in the nearest vicinity of the only Estonian population of *P.* × *italica* known at present, we regard it here as a vegetatively persistent, not repeatedly born nothospecies rather than an accidental hybrid. According to Matfield *et al.* (1970), *P.* × *italica* is sometimes, but not always, isolated from any other member of the section *Potentilla*.

Our data show that *Potentilla anglica* and *P.* × *italica*, the taxa of hybrid origin, are morphologically well separable from each other and from their putative parents from the statistical point of view. Although *P.* × *italica* is known to be morphologically highly variable, the means of the morphological characters used in the study differ from those of *P. anglica* as well as from those of *P. reptans*, which is genetically very close to *P.* × *italica* (Czapik 1975), and agree well with the morphological data obtained from the Dutch material (Ietswaart & Kliphuis 1985). Ietswaart and Kliphuis (1985) stressed that the exact identification of section *Potentilla* (*Tormentillae*) specimens is sometimes possible only

Table 4. Mean ± standard error of the species characters. *P* = significance level according to univariate ANOVA, other notations as in Table 1.

Character	Species				P
	P. erecta	*P. reptans*	*P. anglica*	*P.* × *italica*	
NOD	2.3 ± 0.1	6.8 ± 0.3	3.3 ± 0.1	2.4 ± 0.3	< 0.001
BRCH	2.0 ± 0.0	1.1 ± 0.0	1.7 ± 0.1	2.3 ± 0.2	< 0.001
HU	2.0 ± 0.0	1.4 ± 0.1	1.8 ± 0.1	1.6 ± 0.1	< 0.001
HL	2.0 ± 0.0	2.1 ± 0.1	1.9 ± 0.1	2.1 ± 0.1	0.043
RL	3.0 ± 0.0	1.8 ± 0.1	1.9 ± 0.1	2.2 ± 0.1	< 0.001
FLWS	10.4 ± 0.6	3.9 ± 0.2	5.9 ± 0.7	11.4 ± 1.6	< 0.001
LFL	23.3 ± 0.4	25.9 ± 1.2	16.6 ± 0.7	30.3 ± 2.7	< 0.001
LFW	7.6 ± 0.2	11.0 ± 0.5	7.6 ± 0.4	12.2 ± 1.5	< 0.001
TEETH	9.7 ± 0.5	16.2 ± 0.4	8.9 ± 0.2	15.1 ± 0.6	< 0.001
STPL	12.4 ± 0.2	8.2 ± 0.3	8.3 ± 0.3	13.1 ± 1.3	< 0.001
STPW	9.4 ± 0.2	3.1 ± 0.1	2.3 ± 0.1	4.7 ± 0.4	< 0.001
TOL	2.6 ± 0.1	1.6 ± 0.1	3.2 ± 0.1	3.5 ± 0.3	< 0.001
TOW	1.2 ± 0.0	1.3 ± 0.1	1.7 ± 0.1	2.1 ± 0.1	< 0.001
SEPL	3.1 ± 0.0	8.0 ± 0.2	4.2 ± 0.1	5.2 ± 0.2	< 0.001
SEPW	1.5 ± 0.0	3.4 ± 0.1	2.3 ± 0.0	3.0 ± 0.1	< 0.001
LFN	3.0 ± 0.0	5.2 ± 0.1	3.1 ± 0.0	4.6 ± 0.1	< 0.001
PET	0.1 ± 0.0	5.0 ± 0.4	1.5 ± 0.1	3.8 ± 0.5	< 0.001
LPET	3.8 ± 0.1	8.5 ± 0.2	5.8 ± 0.1	7.1 ± 0.3	< 0.001
WPET	3.5 ± 0.1	7.1 ± 0.1	5.7 ± 0.1	6.7 ± 0.2	< 0.001

with the aid of the data of chromosome numbers and fertility degree. Hence, as Estonian *P.* × *italica* produces no seeds and is hexaploid (2n = 42), the studied plants definitely belong to this nothospecies.

The variation of *Potentilla reptans* is not very wide, as its subclusters of level III did not appear separated on the scatterplot (Figs. 2 and 3), but were situated within each other, while the subclusters of level IV were mutually indistinct.

Morphological differences in *Potentilla anglica* are not important either (being even smaller than in *P. reptans*), as the subclusters of level IV appeared indistinct and revealed no subgroups on the ordination scheme; still, specimens originating from different regions were clustered into separate subclusters. Hence, the existence of geographic morphotypes of *P. anglica* is possible and needs further consideration.

The specimens identified as *Potentilla erecta* var. *erecta* and *P. erecta* var. *strictissima* (some authors have considered these taxa subspecies or even species) did not form clusters of their own either when the intraspecific variation of *P. erecta* was analysed (Leht & Paal 1998b) or when their variation was studied in comparison with *P. reptans*, *P. anglica* and *P.* × *italica* (Fig. 1). At the same time, *P. reptans*, *P. anglica* and *P.* × *italica* formed clusters consisting of only one taxon. As the subtaxa of *P. erecta* did not cluster out even as small indistinct groups on level IV, it confirms once more that these subtaxa do not deserve the rank of subspecies but should be referred to as varieties.

Hence, as in the analysis *Potentilla* × *italica* behaved in the same way as the "good species" *P. reptans* and the stabilized hybrid species *P. anglica*, which each formed a separate cluster, it is certainly justified to recognize it at the same taxonomic level as *P. reptans* and *P. anglica*, i.e., as a morphologically stable nothospecies.

Acknowledgements

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