

Taxonomic status of *Saussurea alpina* subsp. *esthonica* (Asteraceae): phenetical analysis

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Morphological variation of *Saussurea esthonica* Baer ex Rupr. and *S. alpina* (L.) DC. s. str. was studied with different multivariate methods. The most important characters supporting the clustering of the specimens into groups are the shoot height and characters correlated to it, and hairiness of leaves, while the type of trichomes in both taxa is the same. Hence, these characters depend very much on ecological conditions and are, therefore, taxonomically not reliable enough. It appeared also that several specimens were morphologically intermediate between typical representatives of *S. esthonica* and *S. alpina* s.str. Therefore, we consider it more appropriate to treat these taxa as ecogeographical subspecies: *S. alpina* subsp. *esthonica* (Baer ex Rupr.) Kupff. and *S. alpina* subsp. *alpina*. Chromosome numbers established for *S. alpina* subsp. *esthonica* are $2n = 52, 54$.

Keywords: chromosome numbers, Estonia, Latvia, morphology, multivariate methods, *Saussurea alpina*, *Saussurea esthonica*

INTRODUCTION

The genus *Saussurea* comprises over 300 species distributed mostly in Asia (Bremer 1994) where, in the Himalayas and high mountains of China, its primary center of diversity lies (Lipschitz 1979). The genus is represented in Europe by three to nine or more species, depending on the species concept used. According to Hegi (1954), only three species occur in Europe: *S. alpina* (L.) DC.,

S. discolor (Willd.) DC. and *S. pygmaea* (Jacq.) Spreng. Lipschitz (1976) added to the list six species found only in the European part of Russia and in the Ukraine. The list becomes even longer, if some subspecies of *S. alpina* are recognized as species.

Saussurea alpina s. lato is a polymorphic arctic-montane species with a disjunct distribution area in Europe and Asia (Hultén & Fries 1986). The only representative of the genus in Estonia

and Latvia is *S. esthonica* Baer ex Rupr., a taxon that has been defined either as a species (Lipschitz 1962, 1979, Üksip 1966, Kuusk 1978, Czerepanov 1995) or a subspecies of *S. alpina* (Kupffer 1902, Hegi 1954, Lipschitz 1976, Jalas 1980). The first data about *S. esthonica* was recorded by Ruprecht (1845), who mentioned that a new *Saussurea* taxon was found from central Estonia by K. E. von Baer in 1844 and described it as a new species. An improved description of *S. esthonica* was published by Meyer (1855). In 1902, Kupffer found that the differences between *S. esthonica* and typical arcto-alpine *S. alpina* were not large enough to justify recognition of two species, and recognized it as a subspecies, *S. alpina* ssp. *esthonica* (Baer ex Rupr.) Kupff.

At that time the nearest known localities of *Saussurea alpina* s. lato were in Russia in the Arkhangelsk and Olonets provinces, and therefore the taxa seemed to be geographically well separated. Later, localities in the Leningrad and Novgorod districts were found, plants from there identified as *S. alpina* s. str. (Juzepchuk 1955, Sokolovskaya 1965). Hence, Lipschitz (1962) stressed that several specimens were morphologically intermediate between *S. alpina* s. str. and *S. esthonica*, and some were so close to *S. esthonica* that they could even be placed in that taxon. And since a race of *S. alpina*, *S. subbendorffii* Herd., which is morphologically very similar to *S. esthonica*, was found growing in East Siberia and Jakutia, Lipschitz has expressed the opinion that *S. esthonica* is not a local Estonian endemic. According to Laasimer (1965), *S. esthonica* originated from mires of the late glacial period and belongs in the group of plants reaching their present localities from the south. Ingelög *et al.* (1993) assume that *S. esthonica* is a neoendemic of the Baltic Sea region.

Saussurea alpina s. lato shows variation especially in the length of the stem, in the shape, size, pubescence and margin of the leaves, in inflorescence type, and in the shape and pubescence of the involucre. The recorded chromosome numbers and ploidy levels of *S. alpina* s. lato are also quite variable: $2n = 26$ (Rostovtseva 1983, Krogulevitch & Rostovtseva 1984, Lid & Lid 1994), $2n = 36$ (Ishikawa 1916, Lid & Lid 1994), $2n = 48$ (Sokolovskaya & Strelkova 1948), $2n = 51-52$ (Favarger 1965), $2n = 52$ (Löve & Löve 1948, Lavrenko *et al.* 1991, Lid & Lid 1994), $2n = 54$

(Sokolovskaya & Strelkova 1960, Morton 1977, Uotila & Pellinen 1985, Lid & Lid 1994), $2n = 72-76$ (Rostovtseva 1979), $2n = 76?$ (Lid & Lid 1994). Chromosome numbers of *S. esthonica* have not been counted.

The aims of the present study were to compare the morphological variation of *Saussurea alpina* s. str. and *S. esthonica* and to answer the following questions:

1. How well can these two taxa be distinguished from the statistical point of view?
2. What is the chromosome number of *S. esthonica*?
3. What is the taxonomic status of *S. esthonica*?
4. Is *S. esthonica* an endemic taxon?

MATERIAL AND METHODS

Morphological variation of *Saussurea esthonica* was studied from 187 plant specimens collected in 1996 from eight Estonian and two Latvian populations, and from 35 specimens (two populations) from the Herbarium of the University of Tartu (TU) (Table 1, Fig. 1). For studying *S. alpina* s. str., 43 specimens were collected in 1996 from two Norwegian populations, 79 were obtained from Krakow from the Herbarium of the Polish Academy of Sciences (KRAM), and 54 specimens from the Herbarium of the Norwegian University of Science and Technology (TRH). The material from KRAM originated mostly from the Tatra Mountains, but also included single specimens collected from Finland, Sweden, Switzerland and western Russia (Novgorod region); all the specimens from KRAM were treated conditionally as representatives of one population. The material from TRH originated mainly from the counties of Sør-Trøndelag and Nord-Trøndelag. Altogether, 222 specimens of *S. esthonica* and 176 specimens of *S. alpina* s. str. were studied using the 26 macromorphological characters most often considered in the diagnoses of *S. alpina* (Table 2). The characters were measured on herbarium material with a binocular microscope MBS-2 and a ruler.

Micromorphological characters were studied with a scanning electron microscope (SEM) in the Centre for Materials Research of Tallinn Technical University. The epidermis from both sides of

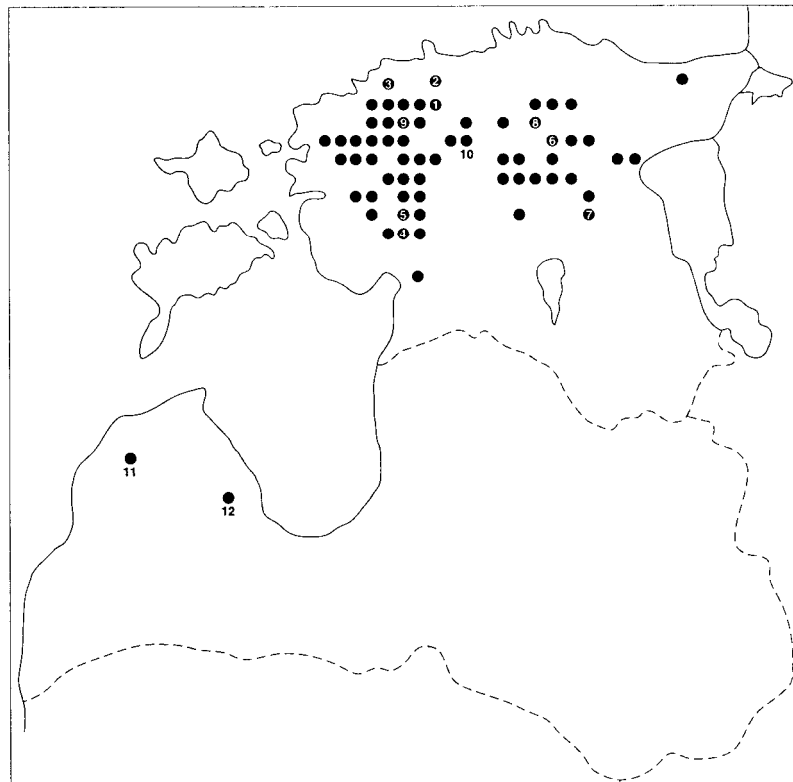


Fig. 1. Distribution of *Saussurea alpina* subsp. *esthonica* in Estonia and Latvia. Studied localities: Tammiku (1), Paraspõllu (2), Niitvälja (3), Halinga (4), Pärnu-Jaagupi (5), Varangu (6), Kalevi (7), Ambla (8), Hageri (9), Viirika (10) in Estonia and Pope (11), Tukums (12) in Latvia.

Table 1. Material studied. Site types of *Saussurea esthonica* named according to Paal (1997). Site types of *S. alpina* s. str. according to Nordhagen (1943).

No.	Locality	Site type	Specimens
<i>S. esthonica</i>			
1.	Estonia, Harjumaa county, Tammiku	Spring fen	21
2.	Estonia, Harjumaa county, Paraspõllu	Spring fen	20
3.	Estonia, Harjumaa county, Niitvälja	Rich paludified grassland	20
4.	Estonia, Pärnumaa county, Halinga	Rich paludified grassland	20
5.	Estonia, Pärnumaa county, Pärnu-Jaagupi	<i>Molinia</i> site type	20
6.	Estonia, Lääne-Virumaa county,	Rich paludified grassland	21
7.	Estonia, Jõgevamaa county, Kalevi	Rich paludified grassland	20
8.	Estonia, Järvamaa county, Ambla (TU)	Rich paludified grassland	21
9.	Estonia, Harjumaa county, Hageri (TU)	Rich paludified grassland	11
10.	Estonia, Raplamaa county, Viirika	Spring fen	21
11.	Latvia, Pope	Rich paludified grassland	5
12.	Latvia, Tuckums county, Tuckums	Rich paludified grassland	20
<i>S. alpina</i> s. str.			
13.	Norway, Sør-Trøndelag county, Oppdal commune, Kongsvoll	Rich, tall-herb birch forest, (trees had been cut) 900 m	30
14.	Norway, Oppland county, Dovre commune, Hjerkin	Minerotrophic, baserich lawn mire, 1000–1200 m	13
15.	Poland, Tatra mountains	1000–1200 m	82
16.	Norway, Sør-Trøndelag and Nord-Trøndelag county	180–750 m	54

one central cauline leaf, the epidermis of involucre, and the surface of the stem of one specimen from each population were examined on air dried herbarium material coated with gold.

For chromosome counts, seeds from three plants from each of the six Estonian populations were collected. Seeds were stratified for three months and germinated at room temperature on moistened filter paper in Petri dishes. Chromosome counts were made from root tips pretreated for 3–4 hours at 15 °C with 0.002% 8-hydroxyquinoline, fixed in Farmer fixative, macerated in 1N HCl at 60 °C for 13–14 minutes, stained with 1% acetoorcein and squashed in acetic acid and glycerin (1:1). The material collected (incl.

voucher specimens) is preserved in the Herbarium of the Institute of Zoology and Botany (TAA).

Data processing

To avoid overweighting, characters strongly depending on ecological conditions in the (micro)habitat — shoot height, length of inflorescence and length of the lowest peduncle — were standardized by range before data processing,

$$x_i' = (x_i - x_{\min}) / (x_{\max} - x_{\min}), \quad (1)$$

where x_{\min} and x_{\max} are the minimum and maximum values of the character.

Table 2. Characters used.

No.	Symbols	Character	Type
1	HSH/R	Height of shoot (cm) standardised by range	metric
2	NLSH	Number of leaves on shoot	count
3	NH	Number of heads (incl. those not flowering yet)	count
4	LI	Length of involucre (cm)	metric
5	WI	Width of involucre (cm)	metric
6	PB	Spot of branching (distance between the topmost inflorescence to the peduncle of the lowest inflorescence): 1 (< 5 cm), 2 (5–10 cm), 3 (15–20cm), 4 (25–30cm)	ordinary
7	NB	Number of branches	count
8	NHSH	Number heads on the shoot	count
9	LIF/R	Length of inflorescence (cm) standardised by range	metric
10	LLP/R	Length of the lowest peduncle (cm) standardised by range	metric
11	LFBL	Length of the fifth basal leaf (cm)	metric
12	WFL	Width of the fifth leaf (cm)	metric
13	BLL	Base of lower leaves: 1: shortly narrowed, 2: slowly narrowed, 3: unnarrowed, 4: clasping	ordinary
14	LUL	Length of the topmost leaf (cm)	metric
15	WUL	Width of the topmost leaf (cm)	metric
16	SC	Stem colour: 1: green, 2: bright red, 3: dark red	ordinary
17	IC	Involucre colour: 1: bright, 2: edges dark, 3: dark	ordinary
18	NTBL	Number of teeth of the fifth basal leaf	count
19	HUPB	Hairiness of upper part of branch: 1: glabrous, 2: few hairs, 3: hairy, 4: very hairy	ordinary
20	HLPB	Hairiness of lower part of branch: 1: glabrous, 2: few hairs, 3: hairy, 4: very hairy	ordinary
21	HI	Hairiness of involucre: 1: glabrous, 2: few hairs, 3: hairy, 4: very hairy	ordinary
22	HUSBL	Hairiness of upper side of the fifth basal leaf: 1: glabrous, 2: few hairs, 3: hairy, 4: very hairy	ordinary
23	HLSBL	Hairiness of lower side of the fifth basal leaf: 1: glabrous, 2: few hairs, 3: hairy, 4: very hairy	ordinary
24	LI/WI	ratio of length and width of involucre	ratio
25	LUL/WUL	ratio of length and width of the topmost leaf	ratio
26	LFBL/WFL	ratio of length and width of the fifth basal leaf	ratio

Cluster analysis was performed with the program package SYN-TAX 5.02 (Podani 1993). The method of incremental sum of squares (MISSQ) with the distance for mixed data (Podani 1994) was used.

For the calculation of common statistics, Spearman rank correlation coefficients between characters were used, and for the evaluation of the importance of characters within clusters by classificatory discriminant analysis, the SAS program package (SAS Institute Inc. 1996) was utilised.

Ordination was carried out with principal component analysis (CANOCO package, version 3.1, Ter Braak 1990; and CANODRAW package, version 3.0, Smilauer 1992) with default parameters settings.

For the estimation of the adjacency of clusters, the distances of all specimens, or operational taxonomic units (OTUs), from all centroids (except the cluster to which the OTU belongs) were calculated according to the postulate that the j th cluster is interpreted as being 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 smaller than the distance to the centroids of all the other clusters (Paal & Kolodyazhnyi 1983, Paal 1994):

$$\min D(x_i, \mathbf{m}_k) = D(x_i, \mathbf{m}_j), \quad (2)$$

$$k, k \neq i$$

where x_i is the vector of OTU x_i , \mathbf{m}_i and \mathbf{m}_j are vectors of the k th and j th cluster's centroid, D = distance (resemblance) function.

To visualise the transitions between the two empirical taxa-clusters *S. esthonica* and *S. alpina* s. str., and to show the distribution of specimens located between the centroids of the clusters considered, the split window method (Parzen 1962) was applied, as in Paal *et al.* (1998). The density of the OTUs projection probability distribution on a straight line passing through the centroids of both clusters was calculated as

$$p(x) = \frac{1}{n} \sum_{i=1}^n \frac{1}{h} \Phi\left(\frac{x-x_i}{h}\right) \quad (3)$$

where $p(x)$ is the distribution density in the point x , Φ is the window function, h is the smoothing

parameter or window breadth, n is the number of OTUs in the cluster, and x_i is the projection of the i th OTU on the line. The density of the normal distribution was regarded as the window function. The smoothing parameter h was calculated according to the formula

$$h = 2s \left(0.05 + \frac{1}{\sqrt{n}} \right) \quad (4)$$

where s is the standard error of the projection.

In order to measure the degree of distinctness of clusters, the α -criterion (Duda & Hart 1976) was used.

$$\alpha = \frac{\left(1 - \frac{2}{\pi d} - \frac{I_2}{I_1} \right)}{\sqrt{2 \left(1 - \frac{8}{\pi^2 d} \right) / nd}} \quad (5)$$

where

$$I_1 = \sum_{x \in X} \|x_i - \mathbf{m}\|^2 \quad (6)$$

$$I_2 = \sum_{i=1}^2 \sum_{x \in X} \|x_i - \mathbf{m}_i\|^2 \quad (7)$$

I_1 is the sum of square distances between the centroid of a united complex of two clusters, I_2 is the sum of square distances between the sample plots and their cluster centroids after dividing the complex into two suboptimal parts, x_i is vector of OUT x_i , \mathbf{m} is vector of the centroid of the united complex, \mathbf{m}_i is vector of the cluster X centroid, d is dimensionality of the united complex, $d = \min(q, n - 1)$, where q and n are the number of characters and specimens in the united complex, respectively.

To acquire a better interpretation of the estimates, it is more convenient to use corresponding probabilities called coefficients of indistinctness (CI) instead of the direct values (Paal 1987, 1994):

$$\text{CI} = \frac{100}{2\pi} \int_{\alpha}^{\infty} \exp\left(-\frac{x^2}{2}\right) dx \quad (8)$$

The last two analyses were made by the original SYNCONT 3.0 program composed by S. Kolodyazhnyi, J. Paal and A. Kink.

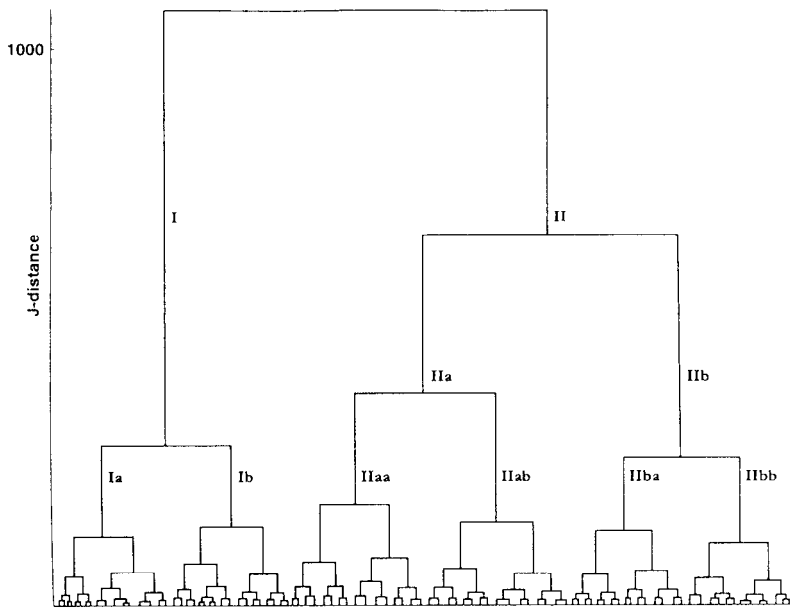


Fig. 2. Dendrogram of *Saussurea alpina* subsp. *esthonica* and *S. alpina* s. str. cluster analysis. The hierarchical levels discussed in the text are marked with Roman numbers and letters.

RESULTS

Chromosome counts

Chromosome numbers were counted in six Estonian spontaneous populations of *Saussurea esthonica*. Populations in Niitvälja, Viirika, Paraspõllu and Kalevi yielded $2n = 52$, in the Pärnu-Jaagupi population the number was $2n = 54$ and in the Tammiku population it could not be precisely determined $2n = 30(?)$.

Clustering

Cluster analysis grouped the data at a quite high level into two unequal clusters (Fig. 2). Cluster I includes the specimens estimated conventionally as belonging to *Saussurea esthonica*. The cluster branches further into two subclusters, Ia and Ib, consisting of representatives of different *S. esthonica* populations. Cluster II also branches further into two subclusters. Subcluster IIa comprises putative intermediate specimens identified as *S. esthonica* or *S. alpina* s. str., while in cluster IIb, specimens of *S. alpina* s. str. prevail.

Also, the principal component analysis demonstrates that the whole sample consists of two

groups corresponding to *Saussurea alpina* s. str. and *S. esthonica*, with several specimens on intermediate positions (Fig. 3). According to the first axis, the characters with the highest scores are the ratio of length and width of the topmost leaf (0.96), height of the shoot (0.64), the width of the topmost leaf (-0.59), the ratio of length and width of the fifth basal leaf (0.55), and the number of branches (0.53). Characters with the highest scores by the second axis are: the number of heads (0.83), the number of branches (0.61), the length of inflorescence standardised by range (0.55), the length of the lowest peduncle (0.45) and the ratio of the length and width of the topmost leaf (0.45).

Conventionally estimated species-clusters of *S. esthonica* and *Saussurea alpina* s. str. were mutually distinct (with coefficient of indistinctness $CI = 0.0$) (Fig. 4), while several pairs of population-clusters were not. Further, the indistinct populations were stepwise joined together until four distinct groups were constituted: cluster 1 includes all populations of *S. esthonica*, cluster 2 contains specimens from the Kongsvoll population (Sør-Trøndelag, Norway) and from TRH (Sør-Trøndelag and Nord-Trøndelag, Norway), cluster 3 is formed by specimens from the Hjerkin population (Oppland, Norway) and cluster 4 by specimens from the Tatra mountains (Poland).

Characters

SEM studies showed that hairs of specimens from both taxa, *Saussurea esthonica* and *S. alpina* s. str., as well as their stomata, are of the same type. Leaves and stems are covered with long, simple, smooth unicellular thin hairs and multicellular thick hairs, multicellular glandular trichomes also occurred. Hairs on involucre are smooth, thin and curved. Differences between the two taxa appeared only in the density of hairs: plants of *S. alpina* are much more hairy. The upper surface of the leaves of *S. esthonica* is either glabrous or with single hairs, the lower surface of some *S. esthonica* specimens is also nearly glabrous while the surfaces of *S. alpina* are always covered with trichomes.

According to the *F*-criterion of discriminant analysis, the most important characters for distinguishing the species are: height of the stem, hairiness of lower surface of the fifth leaf, spot of branch-

Table 3. Importance of characters according to classificatory discriminant analysis. *F*-criterion significance level for all character is below 0.001, except BLL ($p = 0.012$), SC ($p = 0.013$) and LUL ($p = 0.099$). Symbols as in Table 2.

Characters	<i>F</i> -criterion
HSH/R	828.86
HLSBL	299.47
LUL/WUL	223.59
PB	214.83
LLP/R	148.94
LI/WI	141.61
HUSBL	139.25
LIF/R	127.56
HLPB	125.38
LFBL	122.11
NB	118.57
WUL	117.84
HUPB	108.01
NLSH	77.53
IC	50.47
LFBL/WFL	45.44
WI	41.09
NHSH	40.02
WFL	37.63
NLSH	32.70
LI	27.53
HI	14.48
NTBL	13.80
BLL	6.30
SC	6.21
LUL	2.74

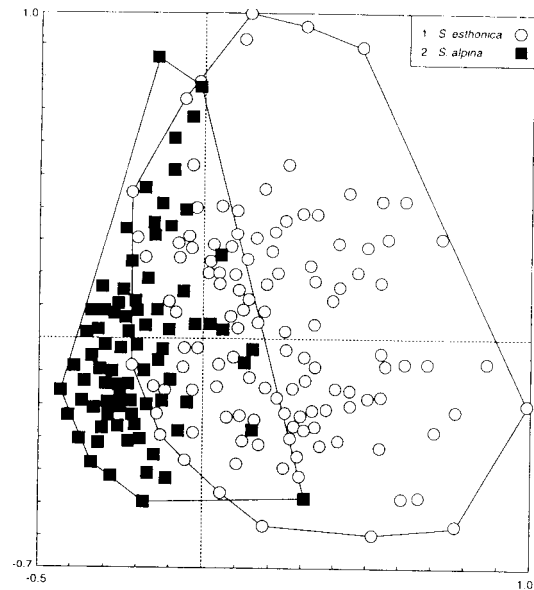


Fig. 3. Classification polygons of conventionally estimated specimens of *Saussurea esthonica* and *S. alpina* s. str. superimposed on to PCA ordination. The first component counts for 48.6% of the variation and the second component for 17.1%.

ing, number of branches, length of inflorescence and length of the lowest peduncle (Table 3).

According to Spearman's rank correlation coefficient most of the characters are well correlated with each other, uncorrelated are only the colour of the stem and the shape of the leaf base. Length of inflorescence is highly correlated with length of the lowest peduncle ($r = 0.93$), height of the shoot ($r = 0.75$), spot of branching ($r = 0.81$), number of branches ($r = 0.79$) and number of heads ($r = 0.66$). Number of branches is also strongly correlated with spot of branching ($r = 0.64$) and number of heads ($r = 0.77$). These characters constitute a quite dense correlation group, others stand more or less separately.

Mean height of *Saussurea alpina* s. str. plants (26.6 cm) is smaller than the height of the smallest *S. esthonica* specimens (Table 4). The highest *S. esthonica* plants grow in Pärnu-Jaagupi (mean 74.0 cm), and the smallest in the Hageri population (44.9 cm). The most hairy plants belong to the Kongsvoll population (Norway) and the most glabrous ones to the Pärnu-Jaagupi population (Estonia).

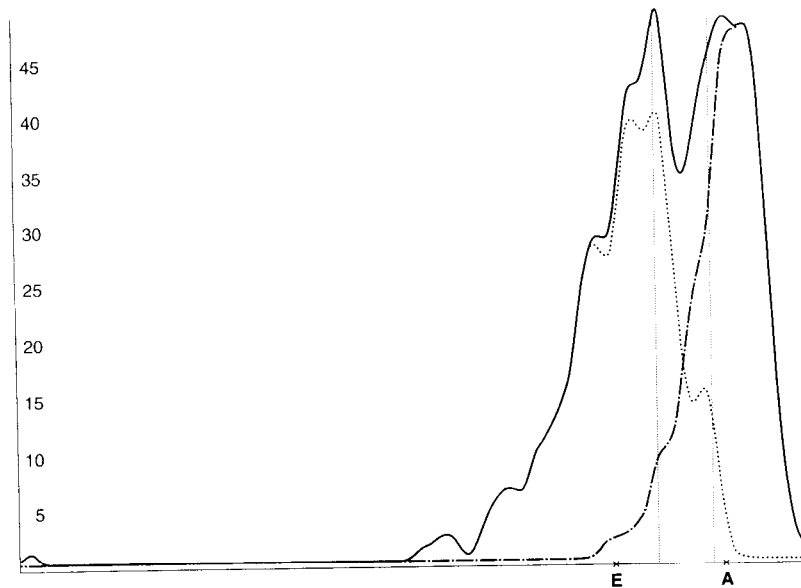


Fig. 4. Specimens projection probability distribution according to the split window method. The curve marked with dots portrays the empirically estimated *Saussurea esthonica* specimens, the curve shown with dash-and-dot line corresponds to the *S. alpina* s. str. specimens. The continuous curve above them represents the joint sample specimens projection probability distribution. *E* and *A* mark the centroids of *S. esthonica* and *S. alpina* s. str., respectively; the dotted lines perpendicular to the line through the cluster centroids delimits the transition zone.

DISCUSSION

According to Favarger (1965), the basic chromosome number in the genus *Saussurea* is $x = 13$. Thus, *S. esthonica* is a tetraploid ($2n = 52, 54$) with a tendency towards aneuploidy.

Lipschitz (1976) states that the polymorphism of West-European *Saussurea alpina* s. lato is partly the result of hybridization with *S. discolor*. Therefore, *S. esthonica* could be an allotetraploid which has arisen from hybridization between diploids of *S. alpina* and *S. discolor* in the overlapping part

of their distribution areas, while later, in the Post Glacial period, as Laasimer (1965) supposed, it spread northwards to Latvia and Estonia. However, taking into account that distances between *S. discolor* and *S. esthonica* areas are large, and that there exists a Siberian taxon *S. stubendorffii* morphologically very close to *S. esthonica* (Lipschitz even considered uniting them), which for geographic reasons cannot have arisen from the hybridization of *S. alpina* and *S. discolor*, we prefer the idea of the endemic origin of *S. esthonica* by the doubling of the chromosomal set of dip-

Table 4. Mean \pm standard deviation of quantitative characters. Symbols as in Table 2.

No.	Character	<i>Saussurea alpina</i>	<i>Saussurea esthonica</i>
1	HSH	26.63 \pm 9.78	64.36 \pm 11.91
2	NLSH	11.67 \pm 2.94	15.44 \pm 4.27
3	NH	6.96 \pm 2.93	10.00 \pm 5.41
4	LI	1.09 \pm 0.09	1.17 \pm 0.17
5	WI	0.88 \pm 0.14	0.77 \pm 0.18
7	NB	2.84 \pm 1.35	4.89 \pm 1.78
8	NHSH	2.85 \pm 1.04	2.09 \pm 0.91
9	LIF	2.47 \pm 1.87	7.69 \pm 5.16
10	LLP	1.58 \pm 1.10	5.22 \pm 3.61
11	LFBL	10.12 \pm 2.56	14.13 \pm 3.65
12	WFL	1.82 \pm 0.57	1.44 \pm 0.62
14	LUL	4.04 \pm 1.29	3.87 \pm 2.02
15	WUL	0.59 \pm 0.32	0.26 \pm 0.23
18	NTBL	13.0 \pm 2.06	14.3 \pm 3.89

loid *S. discolor*. This process may result in a population able to inhabit localities new in comparison with those of its diploid predecessors (Grant 1981). As the maximum elevation in the Baltic region is only 317 m, *S. esthonica* occurs here in conditions quite different from those of the arcto-alpine habitats of typical *S. alpina*: on swampy meadows, wooded meadows, in shrubland and in mires (Kuusk 1978).

Morphologically the specimens clustered clearly into two distinct clusters corresponding to empirically identified *Saussurea esthonica* and *S. alpina* s. str. MISSQ clustering and PCA revealed the existence of intermediates between typical *S. esthonica* and *S. alpina* s. str. specimens (Figs. 2 and 3).

The most important characters in the conventional delimitation of *Saussurea esthonica* and *S. alpina* s. str. were the height of the stem (even despite of standardising this parameter by range) and the hairiness of lower side of the fifth basal leaf (Table 3). Both these characters depend greatly on ecological conditions — light, humidity, etc. Therefore, it is to be expected that *S. esthonica*, which grows in moist places among high grasses or shrubs, is taller than *S. alpina* s. str. growing in mountains in well lit and less humid sites. From the taxonomical point of view height is not considered a reliable character in delimiting taxa. In some cases even definite correlation between the height of the plant and its geographical origin occurred — specimens of more northern origin being considerably lower than those from further south (Rousi 1971). Leaves of *S. alpina* are more hairy than leaves of *S. esthonica*, while their hairs are of the same type. Density of hairs is also a character that depends on habitat conditions: in dry and open windy places plants are more hairy than those growing in shady moist habitats (Rousi 1965). Thus, morphological data taken from specimens growing in different habitats should be used with great care (Øvstedal 1998).

Therefore, since the most important characters supporting the clustering the material into groups are taxonomically not reliable enough and numerous specimens with intermediate characters exist, we cannot recognize these taxa as independent species. Hence, as they are geographically more or less separated and grow in different ecological conditions, we consider it more appropri-

ate to treat these taxa as eco-geographical subspecies: *Saussurea alpina* subsp. *esthonica* (Baer ex Rupr.) Kupff. and *S. alpina* (L.) DC subsp. *alpina*. For more detailed studies growth experiments would be useful — comparison of the morphology of taxa, which originally inhabit ecologically different sites, after cultivation in ecologically identical conditions, could help to decide about the reliability of characters: do they depend on the habitat conditions or not.

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