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MORPHOLOGICAL VARIABILITY OF *PYROLA MINOR* IN SWEDEN, JAPAN AND NORTH AMERICA

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Introduction

Species with a broad distributional pattern may exhibit regional variation that warrants documentation and taxonomic interpretation. One method of assessing this variability is through the analysis of quantitative measurement data for morphological characters across the range of the species as has been done for *Pyrola asarifolia* Michaux[2,6].

Pyrola minor L. is a circumpolar species found primarily in the cool temperate and subarctic regions of the Northern Hemisphere. Because of its unique morphological features, *P. minor* has been treated as the monotypic subgenus *Amelia*[11]. The features that distinguish this species are its short, straight, insert style, stigmatic lobes that arch radially, short anther sacs lacking tubes and bearing large pores represented by the truncated open ends of the sacs, and narrow filaments. The remainder of the species are included within subgenus *Pyrola*. These species have exsert, and generally declinate styles, erect to somewhat divergent stigmatic lobes, and anther sacs with pores at the ends of small tubes, and thicker filaments.

Pyrola minor is known to hybridize with species in the *P. rotundifolia* L.—*P. asarifolia* complex[3,10] and with some species in other sections of the genus[5]. It has been considered to be one of the parents of the Eurasian allotetraploid *P. media* Sw.[9] and is implicated in the origin of the Japanese *P. faurieana* H. Andres (Haber & Takahashi, in prep.).

The present study documents the intraspecific morphological variability of a species of *Pyrola* that holds a unique taxonomic position in the genus and has a broad distributional range and the ability to hybridize with various species in different sections of the subgenus *Pyrola*.

Table 1. Statistical data summary for *Pyrola minor* from five areas in Sweden

Character	1. Southern maritime area					2. Southern area				
	N	X̄	s.d.	X̄±2s.e.	range	N	X̄	s.d.	X̄±2s.e.	range
Scape height (cm)	79	16.95	3.01	16.27-17.63	8.0-24.5	192	18.76	3.42	18.26-19.26	10.3-27.5
Number of flowers	79	12.75	3.49	11.97-13.53	3-20	192	12.79	3.79	12.25-13.33	4-27
Bract length (mm)	9	3.68	0.71	3.20-4.16	2.8-4.6	25	3.73	0.88	3.37-4.09	2.4-6.6
Sepal length (mm)	69	1.20	0.17	1.16-1.24	0.8-1.6	172	1.27	0.19	1.25-1.29	0.8-1.7
Sepal width (mm)	69	1.38	0.19	1.34-1.42	0.8-2.0	172	1.46	0.16	1.44-1.48	1.0-1.9
Petal length (mm)	21	4.12	0.53	3.88-4.36	3.4-5.2	40	4.37	0.49	4.21-4.53	3.6-5.4
Anther length (mm)	67	1.07	0.09	1.05-1.09	0.9-1.3	152	1.05	0.10	1.03-1.07	0.8-1.3
Style length (mm)	51	1.49	0.24	1.43-1.55	1.0-1.9	103	1.58	0.29	1.52-1.64	0.9-2.2
Blade length (cm)	77	3.20	0.68	3.04-3.36	1.2-5.0	192	3.52	0.69	3.42-3.62	2.1-5.9
Blade width (cm)	77	2.39	0.54	2.27-2.51	1.1-3.9	192	2.65	0.51	2.57-2.73	1.6-4.0
Petiole length (cm)	77	2.07	0.71	1.91-2.23	0.6-4.0	192	2.51	0.79	2.39-2.63	1.0-5.2

Table 1. Continued

Character	3. Central-northern maritime area					4. Central mountain area				
	N	X̄	s.d.	X̄±2s.e.	range	N	X̄	s.d.	X̄±2s.e.	range
Scape height (cm)	66	17.64	4.32	16.58-18.70	10.4-28.3	104	16.72	4.52	15.84-17.60	6.6-28.2
Number of flowers	66	12.83	3.27	12.03-13.63	5-20	104	11.85	3.82	11.11-12.59	3-21
Bract length (mm)	10	3.55	0.99	2.93-4.17	2.3-5.4	12	4.28	0.79	3.82-4.74	2.8-5.8
Sepal length (mm)	62	1.25	0.16	1.21-1.29	0.9-1.6	94	1.39	0.20	1.35-1.43	1.0-1.8
Sepal width (mm)	62	1.51	0.16	1.47-1.55	1.2-1.9	94	1.56	0.20	1.52-1.60	1.1-2.0
Petal length (mm)	18	4.69	0.42	4.49-4.89	3.7-5.2	19	4.42	0.39	4.24-4.60	3.7-5.1
Anther length (mm)	51	1.06	0.09	1.04-1.08	0.8-1.2	82	1.10	0.10	1.08-1.12	0.9-1.3
Style length (mm)	32	1.62	0.28	1.52-1.72	1.1-2.1	52	1.68	0.26	1.60-1.76	1.1-2.1
Blade length (cm)	66	3.28	0.65	3.12-3.44	1.9-5.0	104	3.40	0.74	3.26-3.54	1.9-5.8
Blade width (cm)	66	2.57	0.57	2.43-2.71	1.3-4.0	104	2.57	0.65	2.45-2.69	1.2-5.0
Petiole length (cm)	66	2.40	0.88	2.18-2.62	1.0-4.6	104	2.29	0.77	2.13-2.45	0.8-4.5

Table 1. Continued

Character	5. Northern mountain area				
	N	X̄	s.d.	X̄±2s.e.	range
Scape height (cm)	90	12.83	3.53	12.08-13.56	4.4-20.7
Number of flowers	90	9.80	2.67	9.24-10.36	3-16
Bract length (mm)	27	4.02	0.86	3.68-4.36	2.2-5.9
Sepal length (mm)	80	1.40	0.21	1.36-1.44	0.9-1.8
Sepal width (mm)	80	1.63	0.18	1.59-1.67	1.2-2.3
Petal length (mm)	15	4.93	0.48	4.69-5.17	4.0-5.7
Anther length (mm)	77	1.08	0.09	1.06-1.10	0.8-1.3
Style length (mm)	54	1.54	0.30	1.46-1.62	1.0-2.3
Blade length (cm)	90	2.62	0.66	2.48-2.76	1.3-4.4
Blade width (cm)	90	2.01	0.50	1.91-2.11	1.0-3.6
Petiole length (cm)	90	1.47	0.67	1.33-1.61	0.5-3.7

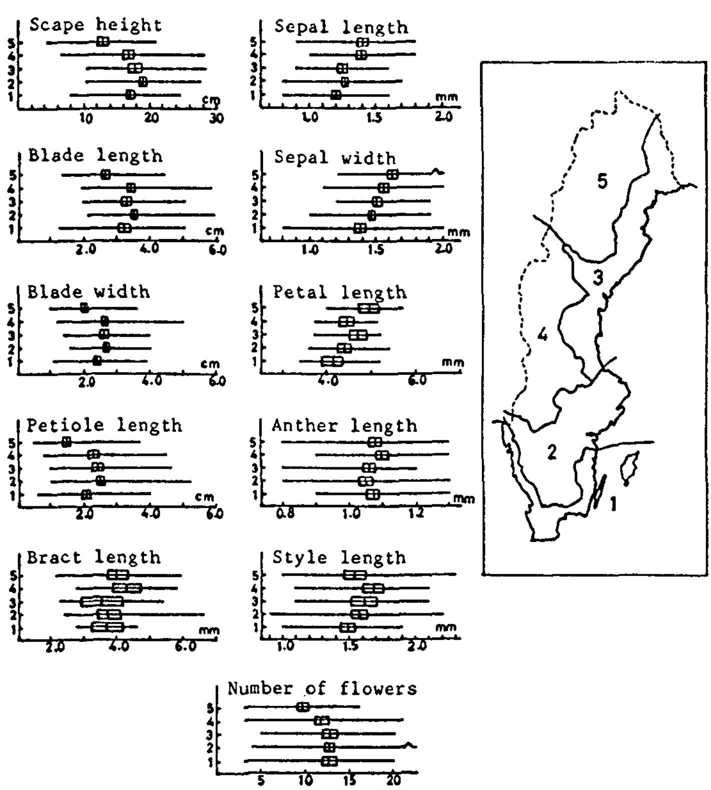

Fig. 1. Variation in the means of 11 morphological characters for *Pyrola minor* from Sweden. Sample numbers 1 to 5 correspond to the numbers on the map. The critical confidence intervals are the lengths of the rectangles, which are delimited by twice the standard error on either side of the means. The horizontal lines represent the measurement ranges.

Table 2. Statistical data summary for *Pyrola minor* from Sweden

Character		N	$\bar{X}$	s.d. (CV)	$\bar{X}\pm2$s.e.	range
Scape height	(cm)	531	16.94	4.25 (25.09)	16.58-17.30	4.4-28.3
Number of flowers		531	12.10	3.68 (30.41)	11.78-12.42	3-27
Bract length	(mm)	83	3.88	0.87 (22.42)	3.68-4.08	2.2-6.6
Sepal length	(mm)	477	1.30	0.20 (15.38)	1.28-1.32	0.8-1.8
Sepal width	(mm)	477	1.50	0.19 (12.67)	1.48-1.52	0.8-2.3
Petal length	(mm)	113	4.46	0.53 (11.88)	4.36-4.56	3.4-5.7
Anther length	(mm)	429	1.07	0.10 (9.35)	1.06-1.08	0.8-1.3
Style length	(mm)	292	1.58	0.28 (17.72)	1.54-1.62	0.9-2.3
Blade length	(cm)	529	3.27	0.76 (23.24)	3.21-3.33	1.2-5.9
Blade width	(cm)	529	2.48	0.59 (23.79)	2.42-2.54	1.0-5.0
Petiole length	(cm)	529	2.21	0.85 (38.46)	2.13-2.29	0.5-5.2

Table 3. Statistical data summary for *Pyrola minor* from Japan and its neighhours

Character		N	$\bar{X}$	s.d. (CV)	$\bar{X}\pm2$s.e.	range
Scape height	(cm)	41	13.60	3.04 (22.39)	12.64-14.56	5.4-20.0
Number of flowers		41	12.10	3.40 (28.08)	11.04-13.16	3-20
Bract length	(mm)	22	4.36	0.98 (22.41)	3.94-4.78	2.8-7.0
Sepal length	(mm)	31	1.36	0.20 (14.58)	1.28-1.44	1.0-1.9
Sepal width	(mm)	31	1.54	0.25 (16.04)	1.46-1.62	1.0-2.0
Petal length	(mm)	19	4.46	0.88 (19.74)	4.06-4.86	2.8-6.0
Anther length	(mm)	36	1.16	0.13 (10.95)	1.12-1.20	0.9-1.4
Style length	(mm)	32	1.63	0.42 (25.80)	1.49-1.77	0.7-2.5
Blade length	(cm)	40	2.68	0.50 (18.68)	2.52-2.84	1.7-3.7
Blade width	(cm)	40	2.20	0.50 (22.90)	2.04-2.36	1.2-3.4
Petiole length	(cm)	40	1.78	0.53 (30.01)	1.62-1.94	0.6-3.0

Table 4. Correlation matrix of 10 morphological characters of *Pyrola minor*

	A	B	C	D	E	F	G	H	I	J
A	1.000									
B	0.473***	1.000								
C	-0.039	0.004	1,000							
D	-0.049	-0.013	0.657***	1.000						
E	-0.188	-0.134	0.563***	0.743***	1.000					
F	0.097	0.135	0.201	0.246	0.285*	1.000				
G	-0.046	0.095	0.204	0.100	0.303*	0.065	1.000			
H	0.664***	0.375**	0.171	0.253*	0.083	0.220	0.105	1.000		
I	0.440***	0.432***	0.136	0.329**	0.151	0.227	0.111	0.816***	1.000	
J	0.672***	0.357**	0.056	0.210	0.054	0.167	0.145	0.778***	0.616***	1.000

Characters : A, Scape height; B, Number of flowers; C, Sepal length; D, Sepal width; E, Petal length; F, Anther length; G, Style length; H, Blade length; I, Blade width; J, Petiole length.
***, P <0.001; **, P <0.01; *, P <0.05.

Materials and Methods

Measurements and counts were made on 531 herbarium specimens of Swedish *P. minor* at UPS. Comparable data were recorded for 41 specimens of Japanese *P. minor* deposited at KYO, S, SAPT, TI, TNS and TUS. The small size of this east Asian sample is due in part to the naturally infrequent occurrence of *P. minor* in Japan and continental east Asia. Measurement data were recorded as outlines in Haber[2].

Swedish specimens were grouped into five geographical samples: 1) southern maritime (Skåne, Blekinge, Öland, Gotland, Halland and Bohuslän), 2) southern (Småland incl. Kalmar, Östergötland, Västergötland incl. Göteborg, Dalsland, Närke, Södermanland, Uppland and Västmanland), 3) central-northern maritime (Gästrikland, Hälsingland, Medelpad, Ångermanland, Västerbotten and Norrbotten), 4) central mountain (Värmland, Dalarna, Härjedalen and Jämtland), and 5) northern mountain (Åsele Lappmark, Lycksele Lappmark, Pite Lappmark, Lule Lappmark and Torne Lappmark) (Fig. 1). The pattern of variation of 11 character means within Sweden was evaluated (Table 1), and the combined values for the whole Sweden were summarized in Table 2. The significance of sample means was judged on the basis of the confidence intervals represented by twice the standard error on either side of the mean (Fig. 1.). The smaller data set of Asian specimens is given in Table 3. Wherever the overlap of confidence intervals warranted, a more precise interpretation of the significance of the two means was obtained by performing t-tests. The correlation coefficient r was determined for 10 character pairs (Table 4). For this calculation 62 specimens having complete data sets for 10 characters were used for Swedish and Japanese samples.

Data for 133 western North American specimens of *P. minor* are given in

Table 5, and those for a sample of 120 eastern North American specimens in Table 6. A total of over 800 herbarium specimens of *P. minor* were examined for this study. The two North American data sets are compared graphically with the Swedish and Japanese samples in Figure 2. Bivariate plots of sample means for leaf blade length and width, sepal length and width are given in Figure 3.

Statistical calculations were performed on an NEC PC-9801Vm using "Multivariate Analysis Library I" by IBC Co. Ltd., Miyazaki, Japan.

The generalized distribution map of *P. minor* in Figure 2 was based on Hultén[8], Haber[3,4] and some additional records.

Results and Discussion

1. Variability of Swedish specimens

Specimens of *P. minor* from the northernmost mountain sample (area 5) have significantly shorter scapes and fewer flowers compared with those further south in Sweden (i.e., areas 1, 2, 4) and in lower elevations, area 3 (Fig. 1). As well, the three leaf characters that were used as a measure of vegetative vigor (blade length and width and petiole length) also have significantly lower means in specimens from area 5. This vegetative dwarfing may be attributable, at least in part, to the shorter growing season at the higher latitude and elevations in this region. In spite of the decreased vegetative vigor and fewer flowers of the northernmost high elevation plants, their flowers are significantly larger than those at least in the southernmost lowland regions (areas 1 and 2), as judged by the means of sepal length and width and petal length. Anthers are relatively small structures in *P. minor* with no significant variation being detected, in part due to limitations in recording the short lengths. No significant differences in the means for style length are evident between adjacent samples (1-2, 2-3, 3-4) although a shift to slightly larger means is evident overall (1-4). Style length for area 5 appears anomalous in that the mean is lower than those for areas 2, 3, and 4 but it too lacks statistical significance.

One can theorize that the increase in flower size with increasing latitude may be, in part, a reflection of coevolutionary pressures that work to promote increased insect visitations in the more harsh northern regions. With increased flower size comes increased visibility to insect pollinators who in general also decrease in numbers at higher latitudes. Insect visitors to species of *Pyrola*, even in more temperate climes, are relatively infrequent (personal observation in eastern North America). This has also been reported for *P. minor* in Greenland[7]. Also, species of *Pyrola*, including *P. minor*, are most commonly selfed (unpublished personal field experimentation and report by Hagerup[7]).

It may, therefore, seem incongruous that flower size should increase northward in *P. minor* if plants tend to be primarily selfed. We have no specific answer to this except to make the further observations that the occurrence of hybrids in various regions of the world and with different species, at least indirectly, attests to facultative entomophily in *P. minor*. It is also known that in high northern latitudes bumblebees tend to be the most common pollinating bees. Kugler[12] has shown that the sense of sight is used by *Bombus* in distance recognition of flowers. Larger flowers would promote outcrossing through increased pollinator visitations. *Pyrola minor* flowers, however, are radially symmetric and relatively closed and drooping and are therefore more highly adapted to selfing than members of subgenus *Pyrola*. In subgenus *Pyrola*, all flowers are bilaterally symmetric and open (crateriform), with some species also having an odor, features characteristic of entomophilous flowers.

The comparatively low means for scape height, blade length and width and petiole length in the southern maritime region of Sweden may very well be due to edaphic factors. Here, as particularly in evidence in Öland and Gotland, shallow soils over limestone bedrock are common. In the eastern Canadian maritime region local species of *Pyrola* are also dwarfed on the shallow soils, over limestone bedrock.

2. Comparison of Swedish, Japanese and North American samples

One of the notable features of the comparison of sample means is the similarity in overall size of the North American plants and the Japanese. Sample means of eastern and western North American plants are statistically indistinguishable from the Japanese sample in scape height, blade length, blade width and petiole length, but differ significantly from the combined Swedish sample means (Fig. 2). Eastern North American plants tend to have more flowers on average than the western but fewer than both Japanese and Swedish plants. North American plants have longer inflorescence bracts than Swedish plants, but do not differ significantly from the Japanese. They also have longer and wider sepals than Japanese and Swedish plants (Figs. 2, 3). In an earlier study of the North American subspecies *P. asarifolia*, ssp. *asarifolia* and its Asian vicariad, ssp. *incarnata* Haber & Takahashi, the north American plants also had wider sepals than the Asian[6]. Petal length (flower size) does not differ among the four samples.

The most distinctive result of this comparison of character means is that anther length is significantly different among the four samples, with that of the Japanese plants being the largest (Fig. 2). Anther length, the presence or absence of tubes, and the size of the pores are some of the more useful key features in *Pyrola*, together with sepal shape and size and the shape and size of the scape bracts. A distinction in style length is evident among the samples, with that of the Japanese and Swedish plants being longer than the North American (Fig. 2). Although style length and shape (straight or declinate) are sometimes used as key characters separating species, they are most useful in distinguishing the

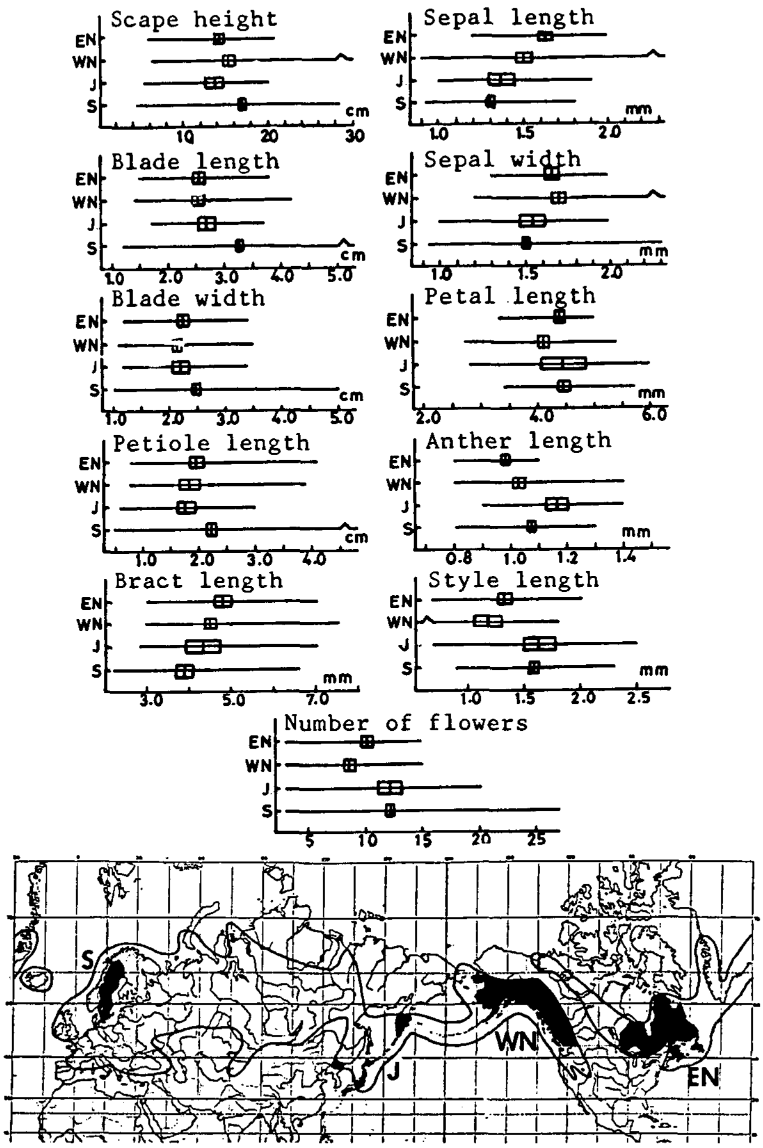

Fig. 2. Variation in the means of 11 morphological characters for *Pyrola minor*. Abbreviations correspond to Swedish (S), Japanese (J), western North American (WN) and eastern North American (EN) samples, respectively. For graphical legend, see Fig. 1.

monotypic subgenus *Amelia* from the rest of the genus (subgenus *Pyrola*), where the styles are exsert and declinate to various degrees. Style form and length are also among the key criteria distinguishing hybrids in which *P. minor* is one of the parents[3].

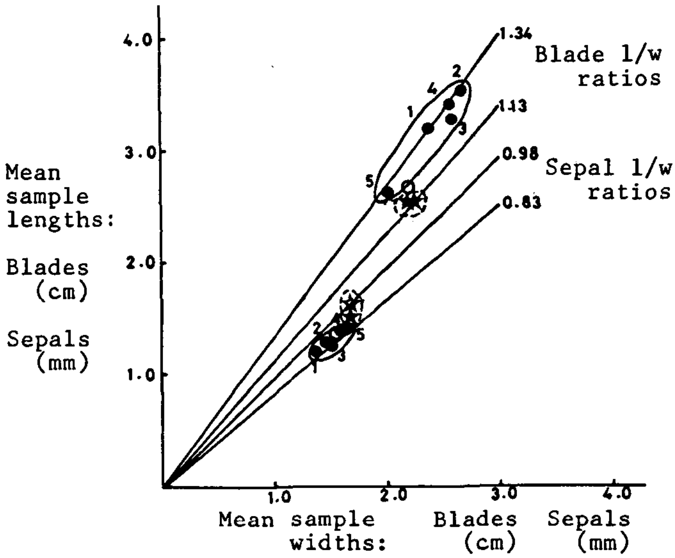

Fig. 3. Bivariate plots of the means for blade and sepal lengths and widths in samples of *Pyrola minor*. The slopes of lines represent the length/width ratios. Swedish means are plotted as solid circles (numbers correspond to the sample numbers in Fig. 1), Japanese means as open circles, western North American means as solid stars and eastern North American means as open stars.

3. Variability and correlation of morphological characters

The coefficients of variation for each character in the four regional samples of *P. minor* are given in Tables 2, 3, 5 and 6. In every region, scape height, number of flowers and the three leaf variables have high coefficients of variation (over 18.0). These characters can be readily influenced by environmental factors such as climate, length of the growing period and soils. The highest coefficients, among all 11 characters examined for all regional samples, were for petiole length. Leaf blade variables appear to be more stable than petiole length. The relatively low coefficients for anther length reflect the low level of variation in this small floral organ and as well the lower degree of accuracy possible in measuring such small structures. The coefficient of variation of style length is also relatively high, being comparable to those of leaf blade variables, or some-

Table 5. Statistical data summary for *Pyrola minor* from western North America

Character		N	$\bar{X}$	s.d.	(CV)	$\bar{X}\pm 2$s.e.	range
Scape height	(cm)	133	15.49	3.93	(25.38)	14.81-16.17	6.2-30.3
Number of flowers		133	8.72	2.48	(28.45)	8.29-9.15	3-15
Bract length	(mm)	126	4.50	0.73	(16.27)	4.37-4.63	3.0-7.3
Sepal length	(mm)	133	1.50	0.26	(17.50)	1.45-1.55	0.9-2.6
Sepal width	(mm)	133	1.69	0.24	(14.25)	1.65-1.73	1.2-2.5
Petal length	(mm)	128	4.11	0.52	(12.55)	4.02-4.20	2.7-5.4
Anther length	(mm)	129	1.03	0.13	(12.58)	1.01-1.05	0.8-1.4
Style length	(mm)	35	1.18	0.37	(31.80)	1.05-1.31	0.5-1.8
Blade length	(cm)	133	2.56	0.57	(22.42)	2.46-2.66	1.4-4.2
Blade width	(cm)	133	2.17	0.49	(22.79)	2.09-2.25	1.2-3.5
Petiole length	(cm)	82	1.86	0.83	(44.62)	1.68-2.04	0.8-3.9

Table 6. Statistical data summary for *Pyrola minor* from eastern North America

Character		N	$\bar{X}$	s.d.	(CV)	$\bar{X}\pm 2$s.e.	range
Scape height	(cm)	103	14.19	3.13	(22.06)	13.57-14.81	5.8-20.8
Number of flowers		103	10.07	2.49	(24.73)	9.59-10.55	3.15
Bract length	(mm)	92	4.79	0.94	(19.62)	4.59-4.99	3.0-7.0
Sepal length	(mm)	103	1.63	0.18	(11.04)	1.59-1.67	1.2-2.0
Sepal width	(mm)	103	1.66	0.18	(10.84)	1.62-1.70	1.3-2.0
Petal length	(mm)	103	4.39	0.42	(9.57)	4.31-4.47	3.3-5.0
Anther length	(mm)	103	0.98	0.05	(5.10)	0.97-0.99	0.8-1.1
Style length	(mm)	120	1.32	0.28	(21.21)	1.26-1.39	0.7-2.0
Blade length	(cm)	103	2.55	0.49	(19.22)	2.45-2.65	1.5-3.8
Blade width	(cm)	103	2.26	0.46	(20.35)	2.16-2.36	1.2-3.4
Petiole length	(cm)	103	1.97	0.60	(30.46)	1.85-2.09	0.8-4.1

times higher, e.g., in the Japanese and western North American samples. This is somewhat unexpected, perhaps mainly because the style is always included and as a resuit, variations in size are normally not readily noticed. In species of the subgenus *Pyrola* where the styles are exsert and declinate, the variation in length is more noticeable. This is particularly so because the length of the style varies with age and maturation of the flower. Recently opened flowers have shorter, less mature styles than those that have been open for several days. This may also be the case in *P. minor*. The values of the coefficients of variation in style length may have been influenced by the different stages in maturity of the opened flowers that were measured.

Comparatively high correlation coefficients are seen in Table 4 between scape height, blade length and width and petiole length. This parallels the results of the graphical presentation of sample statistics for these characters (Fig. 1). Because these characters are correlated and presumably influenced by the same environmental factors, the graphs in Figure 1 show virtually identical patterns in the relationship of the sample means to one another in these characters. The high correlation between sepal length, sepal width and petal length (Table 4), indicators of overall flower size, is also evident in the distributional patterns of the sample means for these characters in Figure 1.

General Discussion

The detailed evaluation of five geographical samples from Sweden indicates that plants from the northernmost region of highest elevations are significantly lower in stature and have the largest flowers compared with plants further south and at lower elevations.

Japanese and North American plants tend to be most similar in size to the northernmost Swedish plants. North American plants have longer and wider sepals than Japanese and Swedish plants, and somewhat shorter anthers and styles and fewer flowers. Although these differences are statistically demonstrable between North American and Eurasian plants, on a practical level, they are not sufficient to warrant the recognition of distinctive taxonomic elements. Infraspecific ranks have not been recognized for *P. minor* by other authors, although an insignificant color variant has been described as *P. rosea* Sm.

Within the Pyroloideae (Ericaceae), the circumboreal *Chimaphila umbellata* exhibits remarkable morphological differentiation between the western North American and east Asian plants[1,14]. In the Monotropoideae (Ericaceae), the circumboreal *Monotropa hypopithys* has different numbers of pollen grain apertures between North American and Eurasian specimens[15]. The intraspecific morphological differentiation between North American and Eurasian *P. minor* demonstrated in the present study parallels the pattern of intraspecific variation evident in some other circumboreal species of the Pyroloideae and

Monotropoideae.

Pyrola minor occurs in North America most commonly im moist and mossy coniferous boreal and montane habitats on a variety of substrates[3]. In Sweden, it grows in comparatively open and wet *Betula* forest, *Salix* thickets and in heath and occurs most commonly in montane and low alpine regions (personal observation in Sweden and Nilsson[13]. It appears to be indifferent to lime content. *Pyrola minor* is rare in Japan, where it grows mainly at the edge of comparatively light subalpine forests of *Betula ermanii* Cham. or *Alnus maximowiczii* Callier, habitats similar to those found in northern Sweden. Over its broad distributional range *P. minor* has adapted to differing habitats with various coniferous dominant forest habitats being occupied in North America and deciduous ones in northern Europe and Japan.

In spite of habitat differences over its broad range and the variations noted in sample means of vegetative and floral characteristics, *P. minor* does not exhibit intraspecific morphological variations of sufficient magnitude to warrant taxonomic recognition.

Summary

Pyrola minor is a circumpolar species mainly of cool temperate to subarctic regions of the Northern Hemisphere. To assess the variability of this widespread species, 11 morphological characters were evaluated on over 800 herbarium specimens from Sweden, Japan and North America. Japanese and North American plants tended to be most similar, and in general, lower in stature and robustness than Swedish plants as seen in scape height, blade length, blade width and petiole length. These vegetative characters have high coefficients of variation, especially in petiole length. These were also shown to be correlated. Japanese and North American plants were most similar in stature to the northernmost mountain sample in Sweden. Within Sweden, plants with the largest flower means are found in the northernmost mountain region. Japanese and Swedish plants differ somewhat from North American plants in sepal length and width, blade and sepal length/width ratios, flower number, anther length and style length. Asian specimens were most distinctive in having the largest anthers. This differentiation in morphological characters in *P. minor* between Eurasia and North America parallels intraspecific differentiation noted for these regions in other circumboreal species of the Pyroloideae and Monotropoideae (Ericaceae). Although statistical differentiation in measurement values for selected characters was demonstrated, on a practical level, they were not of sufficient magnitude to merit taxonomic recognition.

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