

Investigations on the intraspecific variability in *Athyrium filix-femina* (L.) Roth

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Summary : In established populations of *Athyrium filix-femina* (L.) Roth outbreeding is the general rule. Eight populations located in Switzerland were studied using metric and non-metric characters. A considerable polymorphism occurs within the populations. The variability between the populations is — compared to that within the populations — small, but most characters still show statistically significant differences. The origin of this variability is discussed. There is evidence for genecotypic differentiation expressed by physiological adaptation. In contrast to the *A. filix-femina* complex of North America, where four taxa can be separated, the European species shows, following this investigation (of a restricted area), a continuous variability.

Résumé : Dans les populations fixées d'*Athyrium filix-femina* (L.) Roth la fécondation croisée est la règle générale. Huit populations de la Suisse ont été étudiées en utilisant des caractères métriques et descriptifs. Un très grand polymorphisme existe à l'intérieur des populations. La variabilité entre les populations est faible, en comparaison avec celle qui se manifeste à l'intérieur des populations, mais la plupart des caractères montrent cependant des différences statistiquement significatives. L'origine de cette variabilité est discutée. La preuve d'une différenciation genecotypique est expliquée par une adaptation physiologique. A la différence du groupe de *A. filix-femina* de l'Amérique du Nord où quatre taxons peuvent être reconnus, la variabilité des espèces européennes, d'après cette étude (effectuée sur un territoire restreint), est continue.

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In North America LIEW (1972) recognised four different groups within the *Athyrium filix-femina* complex using numerical taxonomic methods. European *A. filix-femina* also shows a considerable intraspecific variability which is reflected in the description of many varieties (MOORE, 1860 ; LUERSSEN, 1889).

In contrast to the flowering plants, the ferns offer less usable characters for population studies. This may also be a reason for the fact that population studies are rarely found in pteridology.

Since *A. filix-femina* shows a very wide ecological tolerance which is indicated by its wide geographical distribution (JALAS & SUOMINEN, 1972) one may possibly expect to find ecotypic differentiation with specially adapted populations showing clear morphological differences.

In this study it was of interest to see how the selected metric and non-metric characters are distributed in eight ecologically and/or spatially differentiated populations. It

is also of interest to know relatively how much correspondence or divergence between and within populations can be found.

The possibility of a relationship between the type of variation and the breeding system and dispersal mechanism is discussed.

MATERIAL AND METHODS

All of the leaves used for measurements were fertile. Studies were made in nature and samples of the following populations (see also Fig. 1) were taken (the geographic indications refer to the map series : Landeskarte der Schweiz, 1 : 25,000) :

— *Population a*, Küsnacht, Küssnachtberg; Kt. Zürich. *Picea abies* plantation, 610 m alt., NW-exposed. Population small, with a few hundred individuals, conditions not optimal. Map Albis No. 1111, co-ord. 688 7/241 5. 50 plants measured.

— *Population b*, Küsnacht, Küssnachtberg, Forch; Kt. Zürich. *Picea abies* plantation, 700 m alt., NW-exp. Small population following a small rivulet (3 km E of population a). Map Stäfa, No. 1112, co-ord. 691 5/241 5. 51 plants examined.

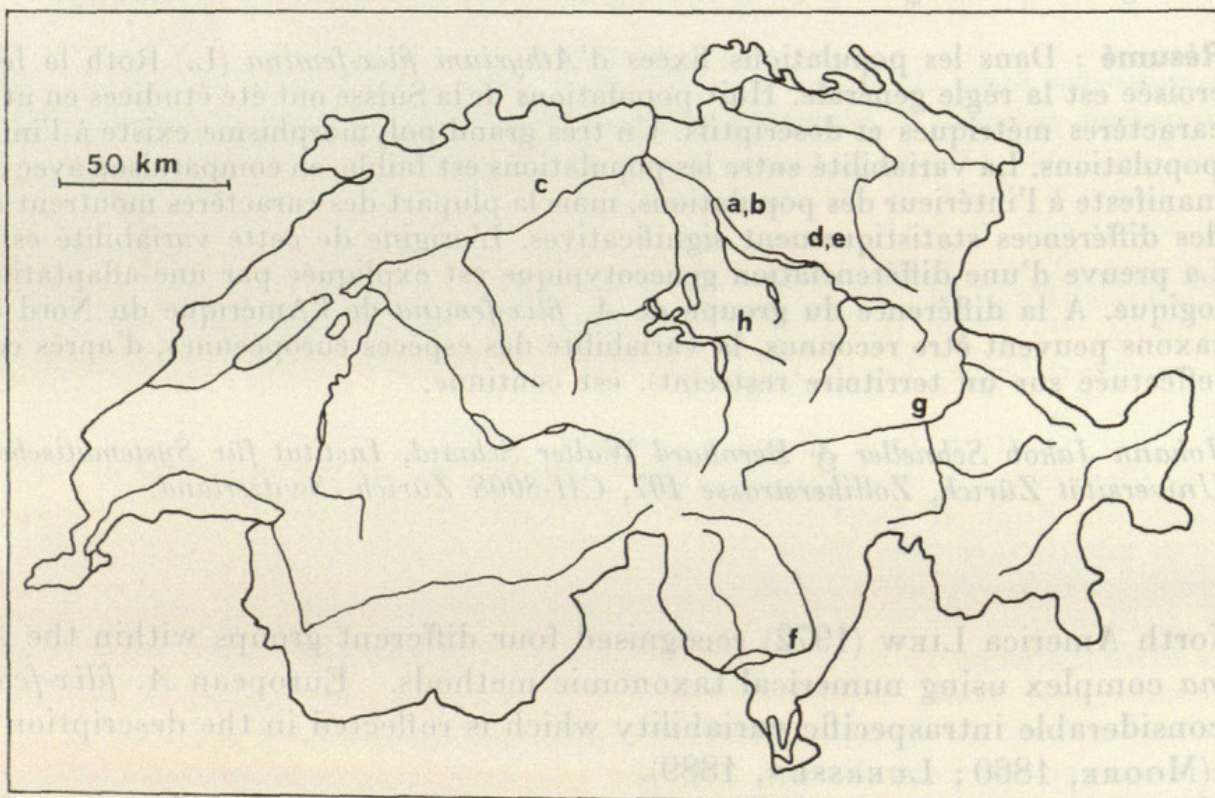


FIG. 1. — Geographical locations of the studied populations.

— *Population c*, Oberbuchsiten, Roggen, Husbrunnen; Kt. Solothurn. *Picea abies* wood, 820 m alt., SE-exp. Small population, more or less isolated by environmental conditions. Slope of Jurassic elevation. Ecological conditions not optimal. Map Murgenthal, No. 1108, co-ord. 623 15/240 2. 51 plants examined.

— *Population d*, Ricken, Bannwald; Kt. St. Gallen. *Picea abies* forest, 825 m alt., NNW-exposed. Dense and large population (part of a continuous population from 800-1250 m alt.)

in optimal environmental conditions. Map Ricken, No. 1113, co-ord. 721 15/234 9. 51 plants measured.

— *Population e*, Ricken, Egg; Kt. St. Gallen. *Picea abies* forest, 1220 m alt., NNW-exposed. Dense and large population (upper part of continuous population from 800-1250 m alt.), in favourable conditions, sympatric with *A. distentifolium*. Map Ricken, No. 1113, co-ord. 723 25/234 13. 51 plants measured.

— *Population f*, Agarone; Kt. Tessin. Deciduous forest, 420 m alt., S-exposed. Dense but rather small population, wet, nutrient-rich, humid soil near a rivulet. Map Bellinzona, No. 1313, co-ord. 713 7/115 4. 18 plants examined.

— *Population g*, Tamins, Girsch; Kt. Graubünden. *Picea abies* forest mixed with *Fagus sylvatica*, 750 m alt., NNW-exposed. Quite dense population, concentrating in the open part of the forest, in favourable conditions. Map Reichenau, No. 1195, co-ord. 750 25/189 25. 50 plants measured.

— *Population h*, Ibergeregge; Kt. Schwyz. *Picea abies*, 1380 m alt., NW-exp. Not very dense but large population, intermingled with *A. distentifolium*. Map Ibergeregge, No. 1152, co-ord. 699 05/298 1. 51 plants examined.

6 plants (No. Sch- 95-100) collected in spring 1978 in Sicily and cultivated in the Botanic Garden in Zurich were used for comparison with Swiss plants (see discussion page 225).

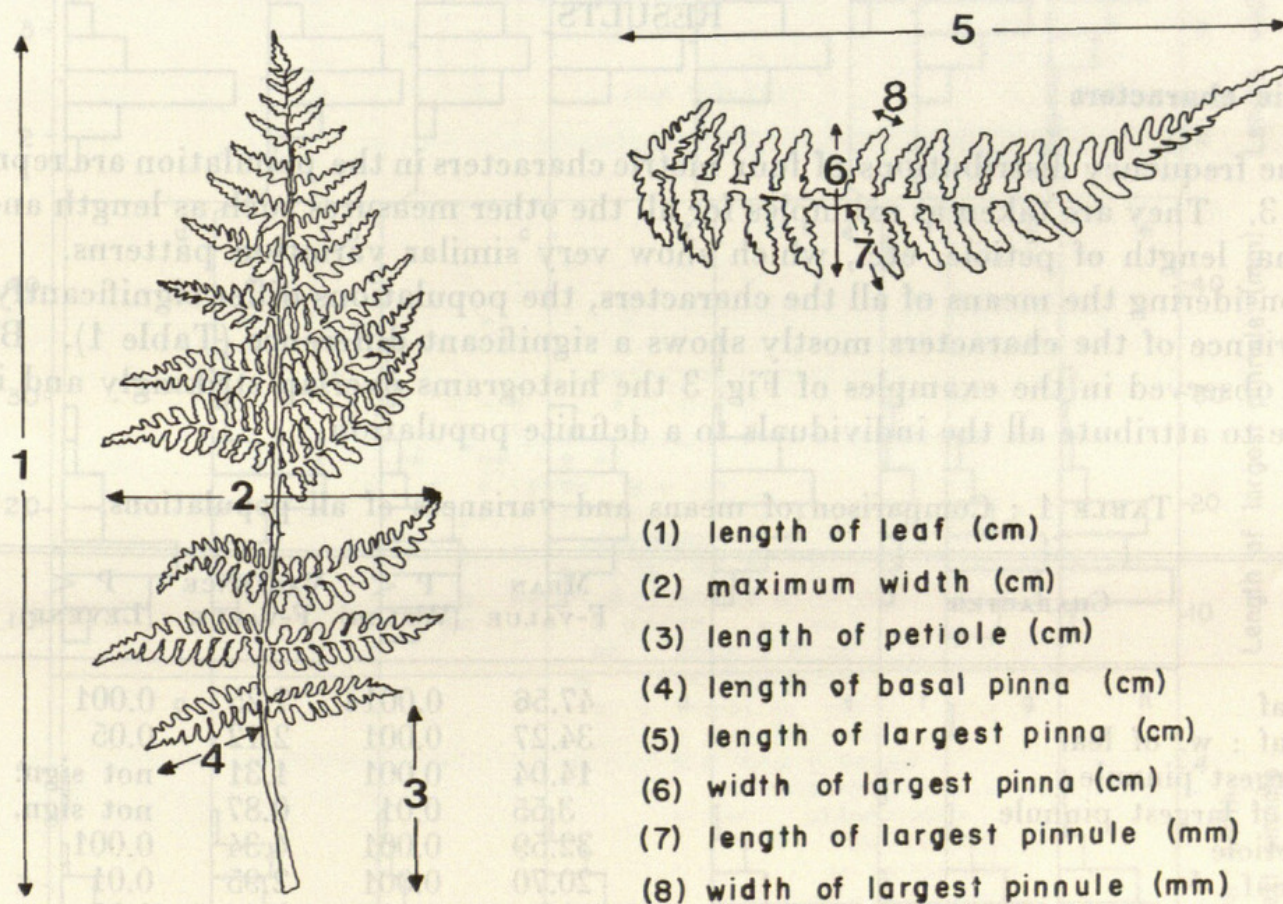


FIG. 2. — Representation of the metric characters.

Representation of metric characters (see Fig. 2).

The non-metric characters used are :

— Rachis colour : green, red.

- Type of distribution of unicellar hairs (“glands”) :
 - 1) Hairs on the adaxial side of the rachis in the blade region.
 - 2) Hairs on the adaxial side of the rachis and petiole.
 - 3) Hairs on the whole leaf (ab- and adaxial, forma *pruinosa*)

— Density of scale pigmentation :

4 categories (see Fig. 6).

— Patterns of scales :

8 types (see Fig. 6).

For the statistical evaluation of the data the following programs developed at the Health Science Computing Facility, UCLA, sponsored by NIH Special Research Resources Grand RR-3, were used (DIXON & BROWN, 1977) :

- BMDP 7D : Description of groups with histograms and analysis of variance (revised Dec. 1977) ;
- BMDP 1F : Two way frequency tables ; measures of association (revised Dec. 1977) ;
- BMDP 6D : Bivariate (scatter) plots (revised Dec. 1977) ;
- BMDP 2M : Cluster analysis of cases (revised Nov. 1978) ;
- BMDP 4M : Factor analysis (revised Nov. 1979).

RESULTS

Metric characters

The frequency distributions of four metric characters in the population are represented in Fig. 3. They are taken as examples for all the other measures such as length and width of pinna, length of petiole, etc., which show very similar variation patterns.

Considering the means of all the characters, the populations differ significantly. Also the variance of the characters mostly shows a significant difference (Table 1). But as it can be observed in the examples of Fig. 3 the histograms overlap strikingly and it is not possible to attribute all the individuals to a definite population.

TABLE 1 : Comparison of means and variances of all populations.

CHARACTER	MEAN F-VALUE	P < (WELCH)	VARIANCE F-VALUE	P < (LEVENE)	} Fig. 3
l. of leaf	47.56	0.001	7.25	0.001	
l. of leaf : w. of leaf	34.27	0.001	2.12	0.05	
l. of largest pinnule	14.04	0.001	1.31	not sign.	
l. : w. of largest pinnule	3.55	0.01	0.87	not sign.	
l. of petiole	32.59	0.001	4.34	0.001	
w. of leaf	20.70	0.001	2.95	0.01	
l. of basal pinna	9.31	0.001	2.21	0.05	
l. of largest pinna	22.67	0.001	6.02	0.001	
w. of largest pinna	14.43	0.001	1.13	not sign.	
w. of largest pinnule	17.87	0.001	2.38	0.05	
l. of leaf : l. of petiole	4.74	0.001	3.24	0.01	
w. of leaf : l. of basal pinna	3.17	0.01	3.74	0.001	
l. of largest pinna : w. of largest pinna	12.38	0.001	0.60	not-sign.	

l. : length ; w. : width.

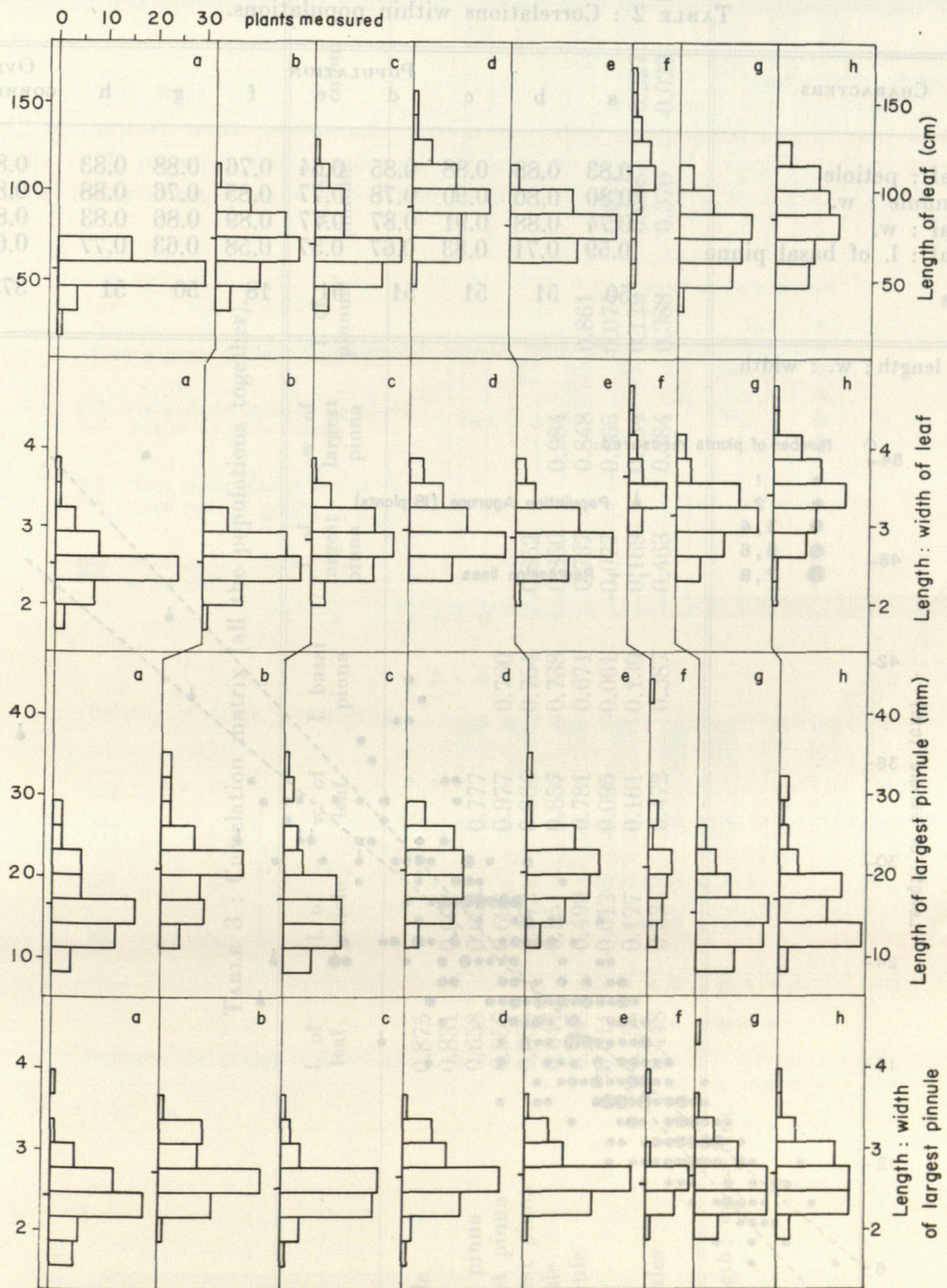


FIG. 3. — Histograms of some metric characters. a, b,... different populations (see material and methods). The mean is indicated by a short line at the base of the histograms.

TABLE 2 : Correlations within populations.

CHARACTERS	POPULATION								OVERALL CORRELATION
	a	b	c	d	e	f	g	h	
l. of leaf : petiole	0.83	0.88	0.88	0.85	0.64	0.76	0.88	0.83	0.875
l. of pinnule : w.	0.80	0.86	0.90	0.78	0.77	0.85	0.76	0.88	0.861
l. of leaf : w.	0.74	0.88	0.91	0.87	0.77	0.89	0.86	0.83	0.832
l. of leaf : l. of basal pinna	0.59	0.71	0.83	0.67	0.57	0.58	0.63	0.77	0.658
Samples	50	51	51	51	51	18	50	51	373

l. : length ; w. : width.

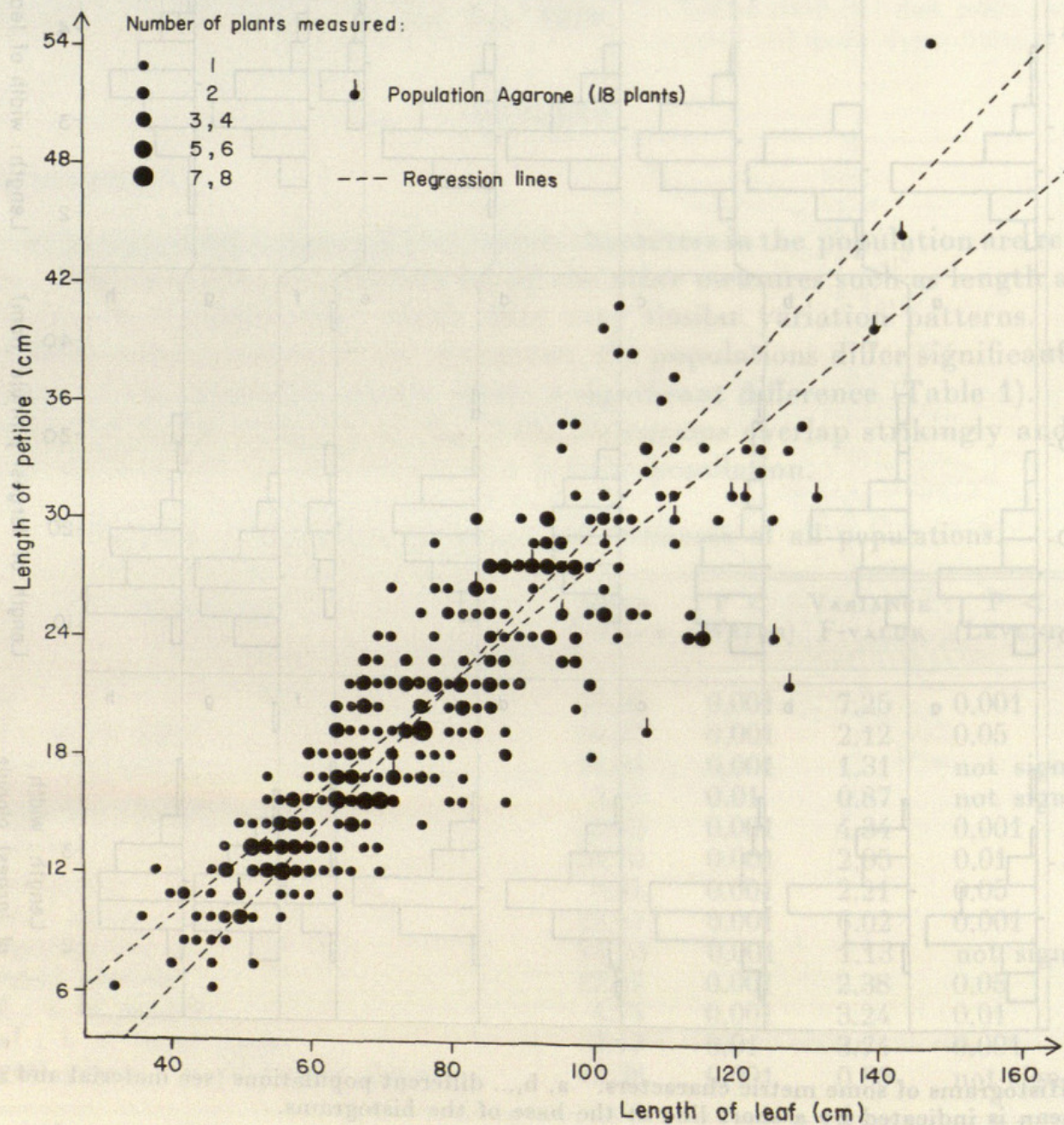


FIG. 4. — Scatter diagram of two metric characters with regression lines.

TABLE 3 : Correlation matrix (all the populations together).

	l. of leaf	l. of petiole	w. of leaf	l. basal pinna	l. of largest pinna	w. of largest pinna	l. of pinnule	w. of pinnule	colour	hairs
l. of petiole	0.875									
w. of leaf	0.831	0.697								
l. of basal pinna	0.658	0.659	0.777							
l. of largest pinna	0.856	0.698	0.977	0.760						
w. of largest pinna	0.665	0.572	0.864	0.754	0.852					
l. of pinnule	0.647	0.551	0.857	0.738	0.850	0.984				
w. of pinnule	0.588	0.499	0.781	0.671	0.767	0.848	0.861			
colour	-0.011	-0.012	-0.095	-0.061	-0.077	-0.065	-0.074	-0.071		
hairs	0.156	0.177	0.161	0.139	0.169	0.134	0.129	0.088	0.227	
density scales	0.448	0.334	0.472	0.387	0.463	0.384	0.388	0.370	-0.022	0.106

l. : length ; w. : width.

All the metric characters are strongly correlated (Table 2, 3, correlation matrix). As examples the two scatter diagrams Fig. 4 and 5 illustrate this markedly for all the others.

Non-metric characters

It was possible to distinguish four non-metric characters, their frequency distribution can be seen in Fig. 6. There is no considerable correlation between these characters and the metric characters with the exception of density of scale pigmentation (Fig. 6 (3), Table 3).

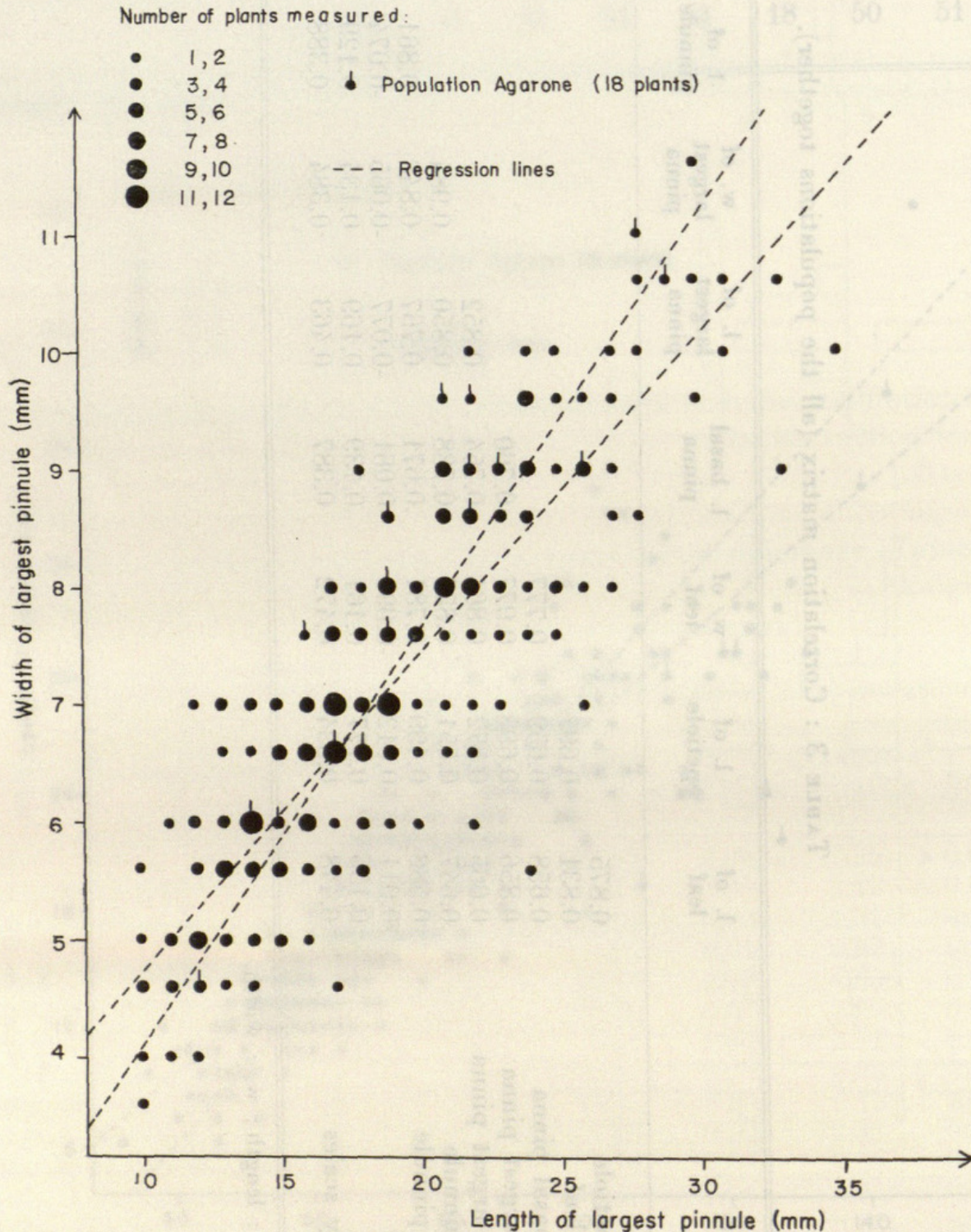


FIG. 5. — Scatter diagram of two metric characters with regression lines.

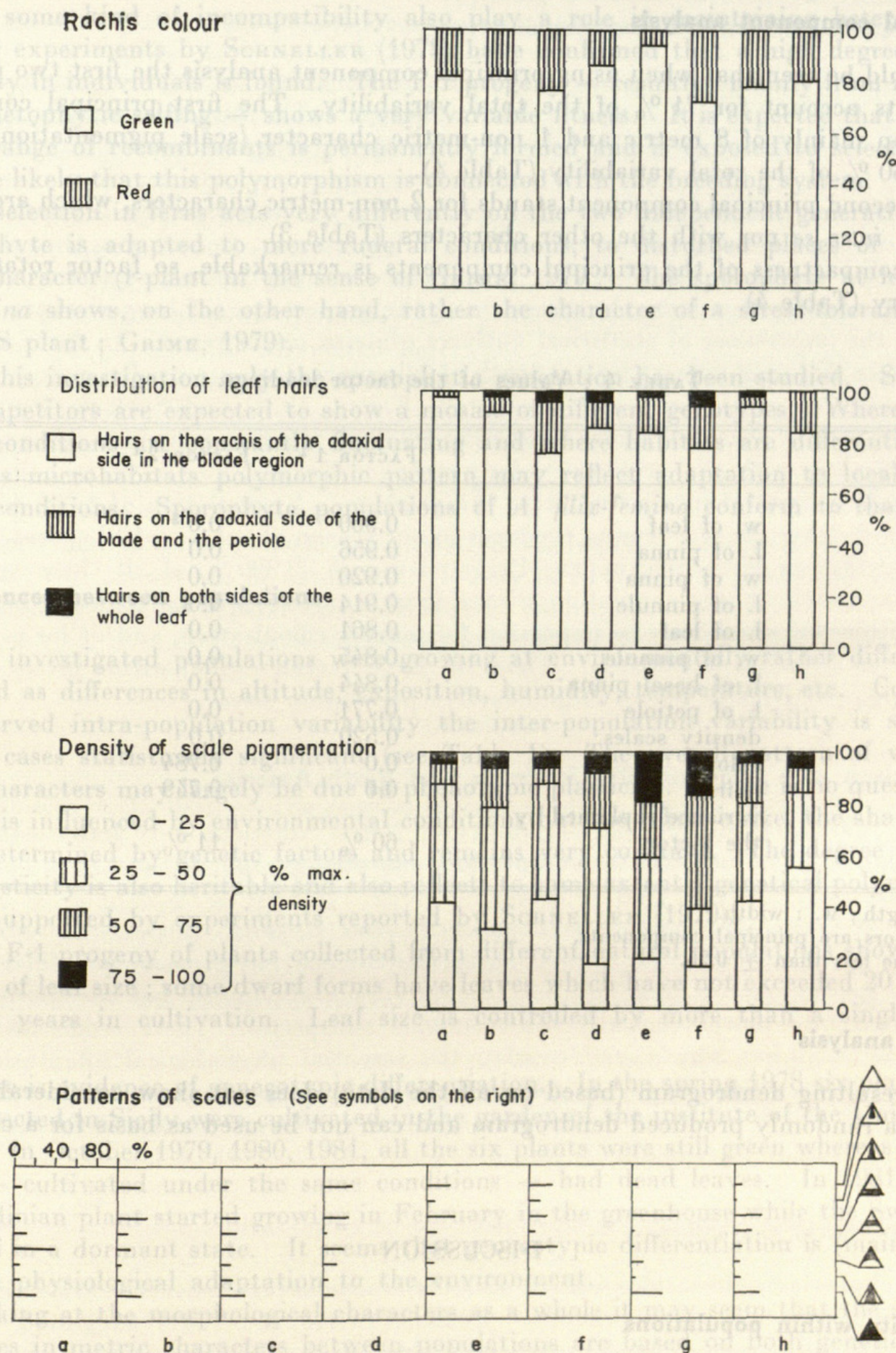


FIG. 6. — Distribution of non-metric characters in the different populations (a, b,...).

Principal component analysis

It could be seen that when using principal component analysis the first two principal components account for 71 % of the total variability. The first principal component is made up mainly of 8 metric and 1 non-metric character (scale pigmentation) and it explains 60 % of the total variability (Table 4).

The second principal component stands for 2 non-metric characters, which are neither correlated *inter se* nor with the other characters (Table 3).

The compactness of the principal components is remarkable, so factor rotation was unnecessary (Table 4).

TABLE 4 : Values of the factor loadings.

	FACTOR 1 ¹	FACTOR 2 ¹
w. of leaf	0.960	0.0 ²
l. of pinna	0.956	0.0
w. of pinna	0.920	0.0
l. of pinnule	0.914	0.0
l. of leaf	0.861	0.0
w. of pinnule	0.845	0.0
l. of basal pinna	0.844	0.0
l. of petiole	0.771	0.0
density scales	0.520	0.0
colour	0.0	0.784
hairs	0.0	0.749
variance explained by the factor	60 %	11 %

l. : length ; w. : width.

1. Factors are principal components.

2. Value less than ± 0.25 .

Cluster analysis

The resulting dendrogram (based on all the data) does not show considerable differences to a randomly produced dendrogram and can not be used as basis for a classification.

DISCUSSION

Variability within populations

A. filix-femina shows considerable polymorphism within populations. The genetic recombination is to some extent controlled by an antheridiogen-system which promotes

the formation of unisexual (male) prothalli (SCHNELLER, 1979). The genetic load and perhaps some kind of incompatibility also play a role in maintaining heterozygosity. Breeding experiments by SCHNELLER (1979) have confirmed that a high degree of heterozygosity in individuals is found. The F₁ progeny — resulting mainly from intra- and intergametophytic selfing — shows a very variable fitness. It is expected that in nature a wide range of recombinants is permanently formed and is exposed to selection; it is therefore likely that this polymorphism is connected with the breeding system. However, natural selection in ferns acts very differently on the two independent generations. The gametophyte is adapted to more ruderal conditions, to disturbed places of microecological character (r-plant in the sense of GRIME, 1979). The sporophyte at least of *A. filix-femina* shows, on the other hand, rather the character of a stress-tolerant competitor (C-S plant; GRIME, 1979).

In this investigation only the sporophytic generation has been studied. Stress-tolerant competitors are expected to show a mosaic of different genotypes. Where environmental conditions are constantly fluctuating and where habitats are differentiated into numerous microhabitats polymorphic pattern may reflect adaptation to local environmental conditions. Sporophyte populations of *A. filix-femina* conform to that scheme.

Differences between populations

The investigated populations were growing at environmentally rather different sites expressed as differences in altitude, exposition, humidity, temperature, etc. Considering the observed intra-population variability the inter-population variability is small, but in most cases statistically significant (see Table 1). The overall pattern of variability of size characters may largely be due to phenotypic plasticity. There is no question that leaf size is influenced by environmental conditions but the relative size, the shape, of the leaf is determined by genetic factors and remains very constant. The degree of phenotypic plasticity is also heritable and also reflects to some extent a genetical polymorphism. This is supported by experiments reported by SCHNELLER (1979).

The F-1 progeny of plants collected from different natural populations shows a great variance of leaf size; some dwarf forms have leaves which have not exceeded 20 cm length after six years in cultivation. Leaf size is controlled by more than a single pair of alleles.

There is evidence of genecotypic differentiation. In the spring 1978 six plants which were collected in Sicily were cultivated in the garden of the institute of the University of Zurich. In October 1979, 1980, 1981, all the six plants were still green whereas the Swiss plants — cultivated under the same conditions — had dead leaves. In 1981 offspring of a Sardinian plant started growing in February in the greenhouse while the Swiss plants were still in a dormant state. It seems that genecotypic differentiation is (mainly) manifested in physiological adaptation to the environment.

Looking at the morphological characters as a whole it may seem that the significant differences in metric characters between populations are based on both genetic differentiation and phenotypic plasticity. But one has to bear in mind also that our samples were taken from a restricted area compared to the whole distribution of the species.

Gene flow within and between populations

EHRlich & RAVEN (1969) have stressed that gene flow in flowering plants is much more restricted in distance than previously thought. The dispersal of fern spores like that of many diaspores in higher plants is leptokurtic (SCHNELLER, 1975; RAYNOR & *al.*, 1976; CONANT, 1978). It seems from measurements made by SCHNELLER (1975) that the distance for gene exchange in *A. filix-femina* in one generation is relatively small and should be measured in meters rather than in kilometers. Considering this, the overall polymorphism might be regarded as a consequence of adaptation to microniches as previously discussed. However, the question of the importance of long-distance dispersal as well as the importance of statistical outliers remains unanswered. In ferns successful long-distance dispersal over at least a tenth of kilometer does occur; for example as seen in the studies on recolonization of Krakatau (ERNST, 1934) and Surtsey (FRIDRIKSON, 1975). On both of these volcanoes ferns were amongst the first colonizers after the catastrophe. Dealing with the problem of long distance dispersal we have to consider also the immense amount of spores that ferns can produce. A population of 1,000 adult ferns of the size of *Athyrium filix-femina* produces in one season about 5×10^{11} spores (approximative calculation after SCHNELLER, 1975). Even if 99.999 % of all these spores fall within close vicinity of the population, a considerable amount will still be available for long distance dispersal, which may be important for pioneer colonisation, and/or for gene transport between different populations. Thus, the large overall — and within group — variability might, partly, also reflect large effective population sizes.

Comparison with *Athyrium filix-femina* s.l. of North America

LIEW (1972) has studied the variability of North American lady ferns using numerical techniques. In contrast to Europe, four morphologically distinct taxa can be distinguished.

The “W-type” (*A. filix-femina* subsp. *cyclosorum* (Rupr.) C. Chr.) seems to be nearest to the European species. In Europe there is evidence for genecotypic differentiation within the species (mainly in adaptation to environmental climate) but the species cannot be separated into morphologically discontinuous subspecies. There seems to exist an overall polymorphism which may overlap the essential physiological adaptations.

This striking difference in the differentiation of *A. filix-femina* (in the wide sense) in Europe and North America may be due to the very different history of the flora during the glacial period.

The non-metric characters

Two characters, the rachis colour and the hairiness are neither correlated *inter se* nor correlated with other characters. ANDERSSON-KOTTÖ (1931) suggested that the occurrence of anthocyanine (red rachis) is controlled by one dominant allele. Crossing experiments by SCHNELLER (unpubl.) have led to the same conclusion. The frequency of the red phenotype in the observed populations is between 5.8 and 27.8 %, the mean

frequency of all the samples is 17.7 %. — Supposing a normal diallelic inheritance, nearly 17 % of the total plants then were heterozygous for the two alleles. This is in good agreement with the results one expects when looking at the breeding system.

The offspring of a pruinose plant (hairs in the whole leaf) from Horgen (No. A-2) did show segregation to “normal type” (hairs on adaxial side of leaf blade only) and “pruinose”. Crossings with the normal type segregate in experiments of SCHNELLER (unpubl.) about 1 : 1. The frequency of “pruinose” which also seems to be controlled by a dominant allele is very low (2.1 % in the mean). The phenotype “pruinose” was found to occur in nearly all the observed populations. Both the frequency of “red rachis” and the frequency of “pruinose” do not differ much in the different populations. “Red rachis” was found in about the same frequency (20 %) in a population in Norway, ca. 1500 km away from the populations considered here.

One could argue that both characters have no selective value and are the phenotypic expression of neutral genes (KIMURA, 1979), but in this case one would expect a greater variance in the frequency distribution unless effective population sizes are large and differences between populations due to genetic random drift are strongly reduced by gene flow between populations.

Pattern and density of scale pigmentation are weakly correlated with the metric characters ; this cannot yet be explained. It may be in some way connected with phenotypic plasticity and/or depend on physiological conditions.

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