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Phenetic relationships in the *Festuca* spp. from Patagonia

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DUBCOVSKY, J., and MARTÍNEZ, A. 1988. Phenetic relationships in the *Festuca* spp. from Patagonia. *Can. J. Bot.* **66**: 468–478.

Forty-two anatomical and exomorphological characters from 16 species and 2 varieties of *Festuca* native from Patagonia were numerically analyzed. Principal components analysis together with cluster analysis arranged 14 taxa into 5 groups (*F. tunicata* and *F. acanthophylla*, group 1; *F. monticola*, *F. thermarum*, and *F. scabriuscula*, group 2; *F. pallescens*, *F. p. var. scabra*, and *F. kurtziana*, group 3; *F. gracillima* and *F. ventanicola*, group 4; and *F. contracta*, *F. rubra* var. *simpliciuscula*, *F. pyrogea*, and *F. magellanica*, group 5; *F. argentina*, *F. purpurascens*, *F. cirrosa*, and *F. pampeana* were not included in any of the groups). Cluster analyses performed on either vegetative or reproductive characters showed that they alone are not enough to summarize variation among these taxa.

DUBCOVSKY, J., et MARTÍNEZ, A. 1988. Phenetic relationships in the *Festuca* spp. from Patagonia. *Can. J. Bot.* **66** : 468–478.

Une analyse numérique de 42 caractères anatomiques et exomorphologiques de 16 espèces et 2 variétés du *Festuca* natives de la Patagonie a été faite. Des analyses en composantes principales et des groupements ont distribué 14 taxons en 5 groupes (*F. tunicata* et *F. acanthophylla*, groupe 1; *F. monticola*, *F. thermarum* et *F. scabriuscula*, groupe 2; *F. pallescens*, *F. p. var. scabra* et *F. kurtziana*, groupe 3; *F. gracillima* et *F. ventanicola*, groupe 4; et *F. contracta*, *F. rubra* var. *simpliciuscula*, *F. pyrogea* et *F. magellanica*, groupe 5; *F. argentina*, *F. purpurascens*, *F. cirrosa* et *F. pampeana* n'étaient inclus dans aucun des groupes. Des groupements effectués sur les caractères soit végétatifs soit reproducteurs ont montré que seuls, ils ne suffisaient pas pour résumer la variation chez ces taxons.

[Traduit par la revue]

Introduction

Festuca is a genus widely spread in both hemispheres, but its origin is probably in the northern hemisphere (Raven and Axelrod 1974). The South American species of *Festuca* are distributed mainly along the Andes from Tierra del Fuego to Colombia. In this wide distribution at least two regions with numerous taxa can be observed. One is restricted to the southern Patagonian Andes (Parodi 1953; Nicora 1978) and the other is located in the central and northern Andes from northwestern Argentina to central Peru (Türpe 1969; Tovar 1972). As far as altitudinal distribution is concerned, festucas can be found at sea level in the southern extreme of South America in Tierra del Fuego (Moore 1983) up to the limit of vegetation (ca. 4000 m) in lower latitudes. All but two of the taxa considered here occur exclusively in Patagonia or floristically related areas (Parodi 1953; Türpe 1969).

Morphologically the Patagonian species exhibit a wide range of variation reflected in such characters as the presence or absence of rhizomes, leaf width, and inflorescence length (Parodi 1953; Nicora 1978; Matthei 1982). In the narrow-leaved taxa of Patagonia, the variation in leaf size, distribution of sclerenchyma in the leaf cross section, and position of the stomata is similar to that found in the taxa living elsewhere (Aiken et al. 1985). This morphological variation, the number of taxa found in Patagonia, and the economic importance of *F. pallescens* as a pasture make these taxa an interesting group for numerical taxonomy studies.

The purpose of this paper is to define numerically the phenetic and evolutionary relationships of the Patagonian taxa. Data were collected to provide evidence on the origin and nature of the native alliances. In addition, reproductive, vegetative, and reproductive plus vegetative characters were compared to assess their taxonomic usefulness. This study also contributes to a better knowledge of phenetic relationships between *F. pal-*

lescens (an important component of natural grasslands) and the rest of the Patagonian taxa.

Materials and methods

The taxa examined are *F. acanthophylla* E. Desv., *F. argentina* (Speg.) Parodi, *F. cirrosa* (Speg.) Parodi, *F. contracta* Kirk., *F. gracillima* J. D. Hook., *F. kurtziana* St-Yves, *F. magellanica* Lam., *F. monticola* Philippi, *F. pallescens* (St-Yves) Parodi, *F. p. var. scabra* (St-Yves) Parodi, *F. pampeana* Speg., *F. purpurascens* Banks et Solander ex J. D. Hook., *F. pyrogea* Spegazzini, *F. rubra* var. *simpliciuscula* Hackel, *F. scabriuscula* Philippi, *F. thermarum* Philippi, *F. tunicata* E. Desv., and *F. ventanicola* Spegazzini.

The entities were identified using the key of Matthei (1982), who described the Chilean species of *Festuca*. The species living only in Argentina were identified with the keys published by Nicora (1978), Parodi (1953), and Türpe (1969).

The voucher specimens examined are kept in the BAA and BACP herbaria. The list of the specimens examined with the localities and the data matrix are contained in two appendices, which have been placed in the Depository of Unpublished Data.¹ They are also available from the authors upon request.

Characters examined

The characters used and their codification are listed in Table 1. They were from 10 specimens per operational taxonomic unit (OTU), except for *F. monticola* (9 individuals), *F. cirrosa*, *F. pampeana*, *F. r. var. simpliciuscula*, *F. thermarum*, and *F. ventanicola* (8 individuals), and *F. tunicata* (7 individuals). The individuals analyzed were from different populations covering the widest range of the geographical distribution.

Forty-two characters were chosen for conducting phenetic studies (18 vegetative: 6 quantitative and 12 qualitative; 24 reproductive: 9 qualitative and 15 quantitative). Analysis of variance for each of the

¹Copies of the appendices may be purchased from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ont., Canada K1A 0S2.

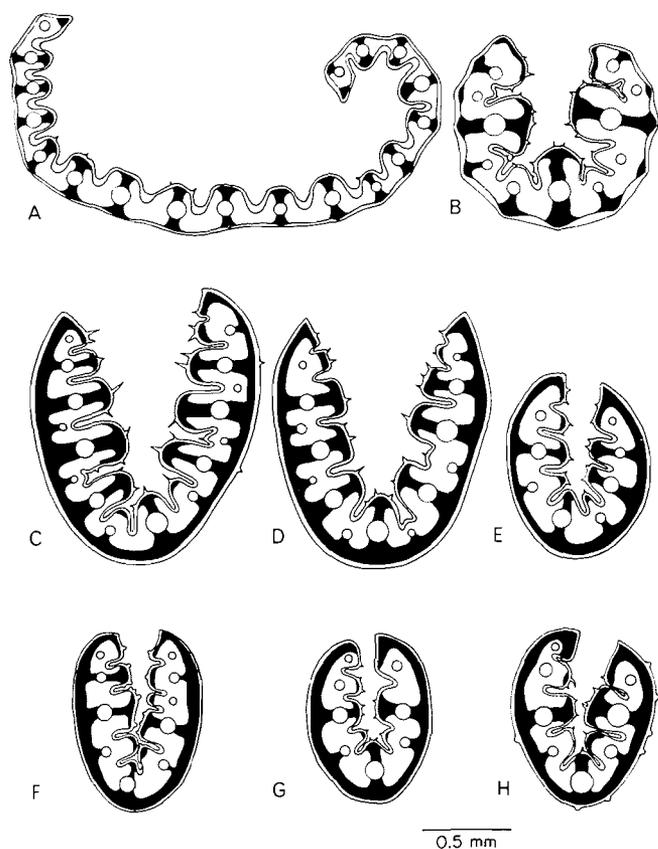


FIG. 1. Block diagrams based on leaf cross sections. (A) *F. purpurascens*; (B) *F. argentina*; (C) *F. tunicata*; (D) *F. acanthophylla*; (E) *F. cirrosa*; (F) *F. monticola*; (G) *F. thermanum*; and (H) *F. scabriuscula*.

quantitative characters of the specimens examined per taxon was conducted because these characters show high intraspecific variation. Characters selected were those with highly significant differences between species ($p < 0.01$). In the case of variation within the qualitative characters an intermediate state between the presence and absence of the character was coded.

Leaf anatomy characters were always observed in the middle region of the blade of the penultimate leaf of an innovation. A cross section of the leaf and an abaxial epidermis preparation of each specimen were made. A cross section of each individual examined was drawn with camera lucida. Based on the drawn cross section a single generalised block diagram was made for each taxon. The diameter and the number of bundles and girders drawn represent the average of the individuals analyzed per taxon.

The basic data matrix consisted of 18 OTUs and 42 characters. After standardization by characters, principal component analysis (PCA) and cluster analysis (CA) were performed. The NT-SYS program (version 4) developed by Rohlf et al. (1982) was used. This program was run in an IBM 370 in the Centro de Tecnología de Sistemas (University of Buenos Aires). A cophenetic correlation coefficient (r) was calculated in all the analyses.

Cluster analyses

Cluster analyses were performed on two different similarity matrices: taxonomic distances and Pearson product moment correlations. Two phenograms were drawn from the OTU-OTU similarity matrix calculated by the unweighted pair group method, using arithmetic averages (UPGMA). The groups of taxa that are present exactly in both phenograms were detected by using the Strict method of the Consensus Program (CP) included in the NT-SYS (Rohlf et al. 1982).

CA was based on the vegetative characters (VChs), reproductive characters (RChs), and VChs plus RChs. The taxonomic distances

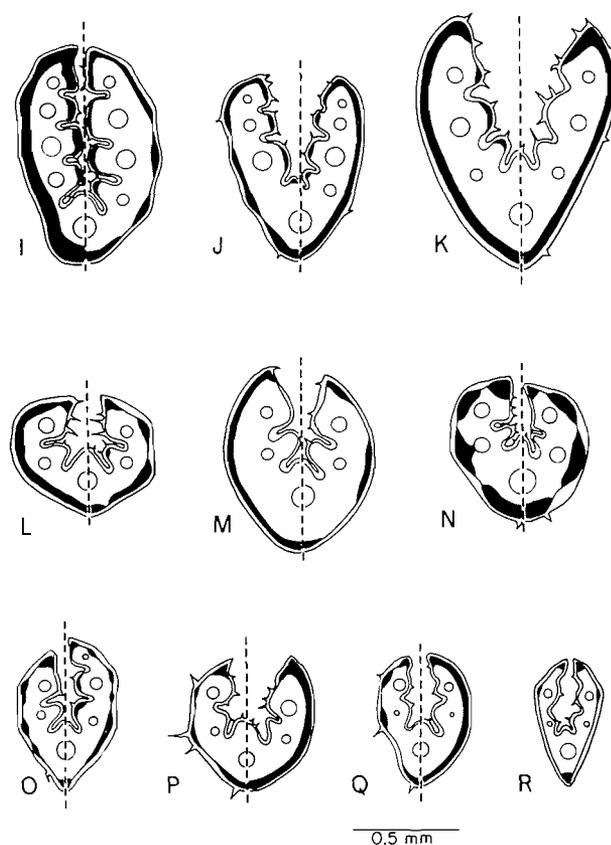


FIG. 2. Block diagrams based on leaf cross sections (I) *F. pallescens*; (J) *F. p.* var. *scabra*; (K) *F. kurtziana*; (L) *F. gracillima*; (M) *F. ventanica*; (N) *F. pampeana*; (O) *F. contracta*; (P) *F. magellanica*; (Q) *F. pyrogea*; and (R) *F. rubra* var. *simpliciuscula*. The broken line separates two aspects of the variation observed in the leaf cross sections.

matrices between VChs and RChs were compared by calculating a cophenetic correlation coefficient. The same coefficient was calculated between the Pearson product moment correlations matrices based on the same sets of characters.

Principal component analysis

PCA was obtained from the correlation matrix based on the standardized data matrix. A tridimensional model of the first three components of the PCA was also drawn. Because of the relatively low fraction of the variation described by them (less than 60%) the ordination efficiency was examined. With this purpose the cophenetic correlation coefficient (r) was calculated by comparing the original taxonomic distance matrix with a Euclidian matrix. The latter matrix is based on the Euclidian distances between all pairs of OTUs in the space defined by the three first components.

Results

Leaf morphology

Fescues vary in internal and external leaf morphology. Figures 1 and 2 show that the 18 taxa studied can be divided into two groups (with no taxonomic value) according to their leaf cross section.

Figure 1 shows the species with adaxial to abaxial girders of sclerenchyma. Six of the taxa also have bands of sclerenchyma tissue under the abaxial epidermis (Figs. 1C, 1D, 1E, 1F, 1G, and 1H). However, *F. cirrosa*, *F. monticola*, *F. thermanum*, and *F. scabriuscula* (Figs. 1E, 1F, 1G, and 1H) can be separated from *F. tunicata* and *F. acanthophylla* (Figs. 1C and

TABLE 1. Characters examined and their codification used in PCA and CA

	State	Code
(A) Vegetative characters		
(1) Rhizomes	Absence	0
	Presence	1
(2) Leaf vernation	Conduplication	0
	Convolute	1
	Absence	0
(3) Anthocyanin in the sheath	Absence or presence	1
	Presence	2
	Absence	0
(4) Sheath with lateral lobes	Absence or presence	1
	Presence	2
	Absence	0
(5) Pulvinus glabrous or pubescent at the base of the lamina	Absence or presence and glabrous	1
	Presence and glabrous	2
	Presence and pubescent	3
	Absence	0
(6) Divergence angle between the blade and the sheath (degree) (Leaf angle of the uppermost leaves in the nonflowered and well-developed tillers was measured with a protractor. For this purpose the leaf angle was that subtended between the proximal 1 cm of the blade and the projection of the sheath axis.)		
(7) Blade length (cm)		
(8) Ligule length (mm)		
(9) Presence of prickles on the abaxial epidermis	Smooth	0
	Smooth or unfrequent prickles	1
	Smooth or frequent prickles	2
	Scabrous	3
	Hairs	0
(10) Presence of hairs or papillae on tyne adaxial epidermis	Papillae	1
	Absence	0
	Absence or presence	1
(11) Presence of short cells in the intercostal abaxial epidermis	Presence	2
	Absence	0
	Absence or presence	1
(12) Presence of stomata in the abaxial epidermis	Absence or presence	1
	Absence	0
(13) Distance between the abaxial midrib and the most distal cell (mm) (Aiken et al. 1985)		
(14) No. of vascular bundles		
(15) Presence of sclerenchyma girders	Absence	0
	Absence or abaxial	0, 5
	Only abaxial	1
	Only abaxial or adabaxial	1, 5
	Adabaxial	2
(16) % girders of sclerenchyma: (no. of adaxial girders + No. of abaxial girders)/(no. of bundles × 2) × 100		
(17) Continuous or discontinuous band of sclerenchyma under the abaxial epidermis	Discontinuous	0
	Usually discontinuous	0, 5
	Discontinuous or continuous	1
	Usually continuous	1, 5
	Continuous	2
(18) Presence of adaxial sclerenchyma	Absence	0
	Rarely presence	1
	Usually presence	2
	Presence	3
(B) Reproductive characters		
(19) Length of culm and inflorescence from the base of the plant (cm)		
(20) Prickles and (or) hairs on the branches of the panicles	Smooth	0
	Smooth or scabrous	1
	Scabrous	2
	Scabrous or hairy	3
	Hairy	4
	Smooth	0
	Smooth or scabrous	1
(21) Prickles and (or) hairs on the culm below inflorescence	Scabrous	2
	Scabrous or hairy	3
	Hairy	4
	Smooth	0
	Smooth or scabrous	1
(22) Culm diameter at panicle base (mm)		
(23) Panicle length (cm)		
(24) No. of spikelets/panicle		

TABLE 1 (concluded)

	State	Code
(25) No. of nodes/panicle		
(26) Spikelet length (mm)		
(27) No. of florets/spikelet		
(28) Length of the first floret (mm)		
(29) Prickles and (or) hairs on the lemma	Smooth	0
	Smooth and scabrous	1
	Scabrous	2
	Hairy	3
(30) Awn length (mm)		
(31) Glume 1 length (mm)		
(32) Glume 1 length/glume 1 full width		
(33) No. of nerves in glume 1		
(34) Ratio between glume 2 length/first floret length	Glume < floret	0
	Glume ≥ floret	1
(35) Length of the second internode of the rachilla (mm)		
(36) Rachilla scabrosity	Smooth	0
	Scabrous	1
(37) Anther length (mm)		
(38) Presence of anthers on the mature caryopsis	Absence	0
	Absence or presence	1
	Presence	2
(39) Lodicule length (mm)		
(40) Lodicule with marginal cilia	Smooth	0
	Ciliate	1
	Glabrous	0
	Glabrous or < 10 hairs	1
	10 to 40 hairs	2
	> 50 hairs	3
(42) Caryopsis length (mm)		

1D) by both the width of the blade and the number of bundles per cross section. *Festuca purpurascens* and *F. argentina* can be segregated from the other six by the absence of sclerenchyma bands under the abaxial leaf surface (Figs. 1A and 1B). The former species has leaves rolled in bud and stomata in the abaxial epidermis, whereas *F. argentina* has leaves folded in bud and no stomata in the abaxial epidermis.

The 10 entities shown in Fig. 2 do not possess girders of sclerenchyma. Five of the species have sclerenchyma under both epidermises (Figs. 2I, 2J, 2K, 2L, and 2O). *Festuca pallens* and *F. p.* var. *scabra* always have sclerenchyma in the ribs under the adaxial epidermis (Figs. 2I and 2J). The percentage of individuals with sclerenchyma under the adaxial epidermis is higher in *F. kurtziana* (80%) than in *F. gracillima* (10%) and *F. contracta* (10%) (Figs. 2K, 2L, and 2O).

The other group of species in Fig. 2 is composed of the taxa without sclerenchyma tissue under the adaxial leaf surface (Figs. 2M, 2N, 2P, 2Q and 2R). *Festuca ventanica*, *F. magellanica*, and *F. pyrogea* possess a continuous or discontinuous band of sclerenchyma under the abaxial epidermis (Figs. 2M, 2P, and 2Q). *Festuca pampeana* is separated from the other three by always having strands of isolated sclerenchyma, with some of the individuals examined having girders of sclerenchyma between the bundles and the abaxial surface (Fig. 2N). *Festuca r.* var. *simpliciuscula* has a discontinuous band and the distribution of this tissue is restricted (Fig. 2R). In addition it is the only species shown in Fig. 2 with stomata in the abaxial leaf epidermis.

Vegetative and reproductive characters

The Patagonian species of *Festuca* show wide variation in

vegetative and in reproductive characters. To test the influence of each set of characters on the phenetic relationships of the species examined here, phenograms based on taxonomic distances, correlation coefficients, and consensus between them were calculated separately for both VChs and RChs.

Figure 3 shows the distribution of the taxa according to their VChs. Consensus analysis reveals three groups. The largest group is composed of *F. contracta*, *F. gracillima*, *F. magellanica*, *F. pyrogea*, *F. r.* var. *simpliciuscula*, and *F. ventanica*. These are the taxa that have the smallest leaves and lack girders of sclerenchyma. A second group of related species consists of *F. thermarum* and *F. scabriuscula* (Fig. 3). The distribution of the sclerenchyma in the leaf cross section and the presence of prickles in the adaxial epidermis separate both species from the other taxa examined here. *Festuca acanthophylla* and *F. tunicata* are also related in the distribution of the sclerenchyma in the leaf cross sections and in the width of the blades, which separate those taxa from the rest (Fig. 3).

The phenograms shown in Fig. 4 are based on RChs. In this case, consensus analysis reveals four groups; again *F. acanthophylla* and *F. tunicata* are grouped together since they share the largest culms and panicles seen in the 18 taxa examined. *Festuca p.* var. *scabra* and *F. kurtziana* are included in the same group because the size of anthers, lemmas, and lodicules is similar in both species.

Festuca monticola and *F. scabriuscula* share a combination of characters that separate them from the rest (i.e., a similar size and number of spikelets per panicle, the number of nodes per panicle, and the presence of more than one nerve in glume 1 in 70% of the individuals examined of *F. scabriuscula* and in 40% of *F. monticola*).

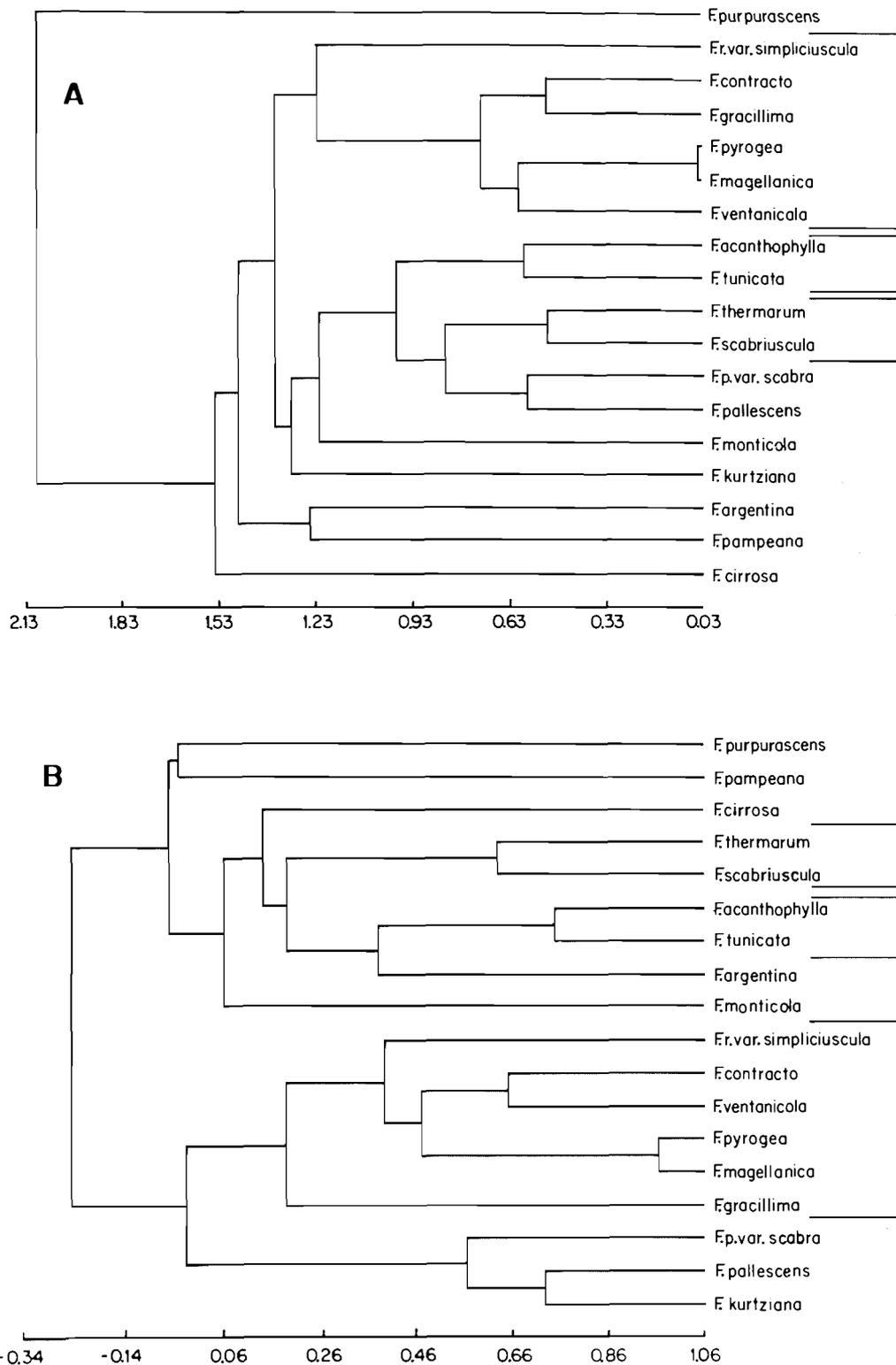


FIG. 3. Phenograms based on vegetative characters. (A) Taxonomic distance ($r = 0.87$); (B) correlation coefficient ($r = 0.77$). The groups were defined by Consensus Program (Strict).

Four species (*F. contracta*, *F. magellanica*, *F. pyrogea*, and *F. r. var. simpliciuscula*) are separated from the rest and included in the same groups by having the shortest culms, spikelets, and anthers (Fig. 4).

The estimation of the cophenetic correlation coefficient between the VChs and RChs gives a quantitative measurement

of the degree of coincidence expressed in phenetic terms between both groups of characters. The coefficient between the Pearson product moment correlation matrices based on VChs and that on RChs was small (0.34). Even smaller (0.18) was that based on the taxonomic distance matrices between VChs and RChs.

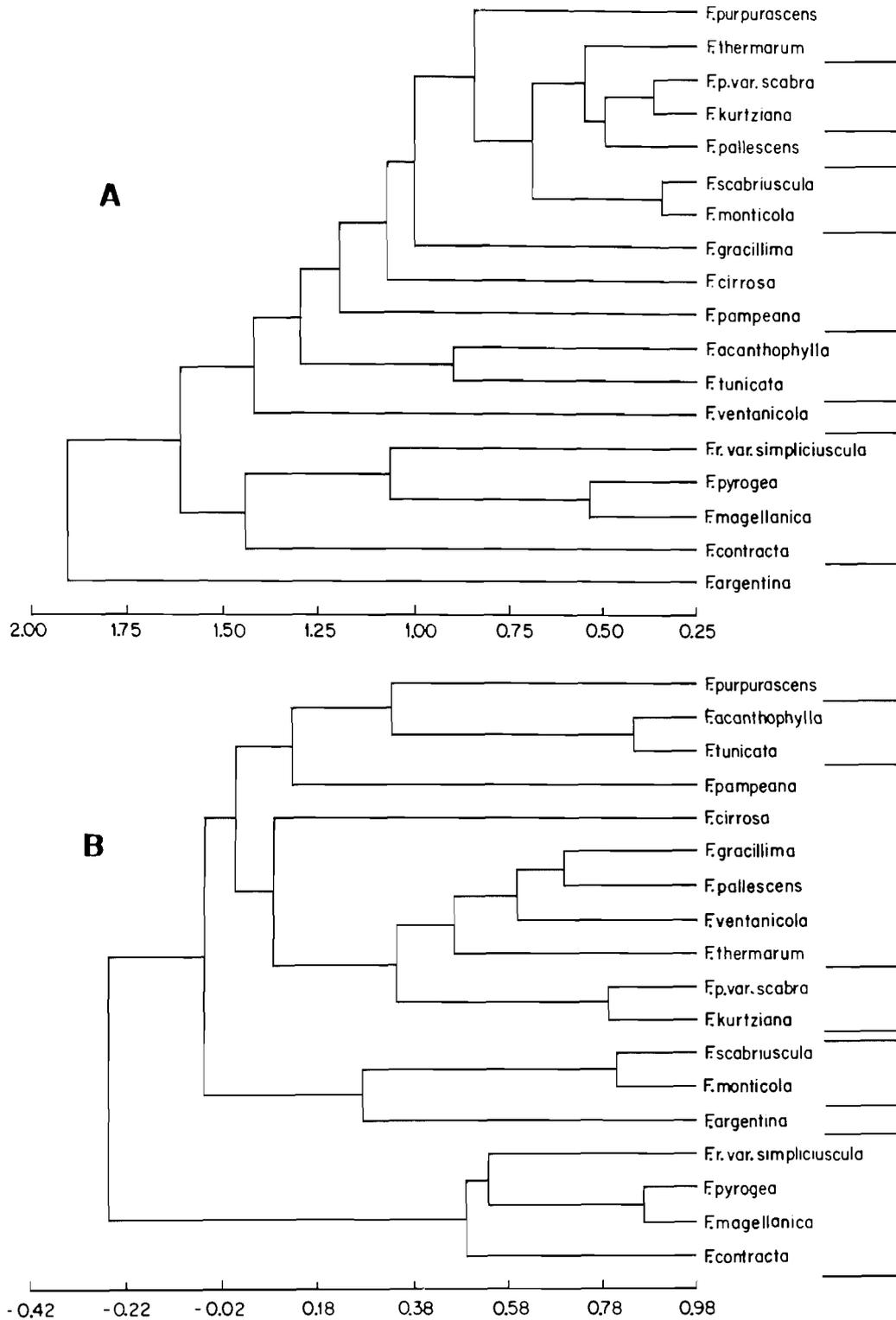


FIG. 4. Phenograms based on reproductive characters. (A) Taxonomic distance ($r = 0.85$); (B) correlation coefficient ($r = 0.81$). The groups were defined by Consensus Program (Strict).

Principal components and cluster analyses

Table 2 describes the contribution of each of the components to the model. Six were chosen because they accounted for a significant portion of the total variation (79.88%).

Figure 5 shows the tridimensional model defined by the three first components. They absorbed 55.59% of the variation, which is relatively low, but the cophenetic correlation

coefficient between this model and the original distance matrix is high ($r = 0.88$).

In Table 3 are displayed the 10 characters with the highest contribution to each one of these components. The number of characters chosen was arbitrary in order to illustrate the nature of the characters that contributed most highly to each component. In the first and third component there are six RChs and

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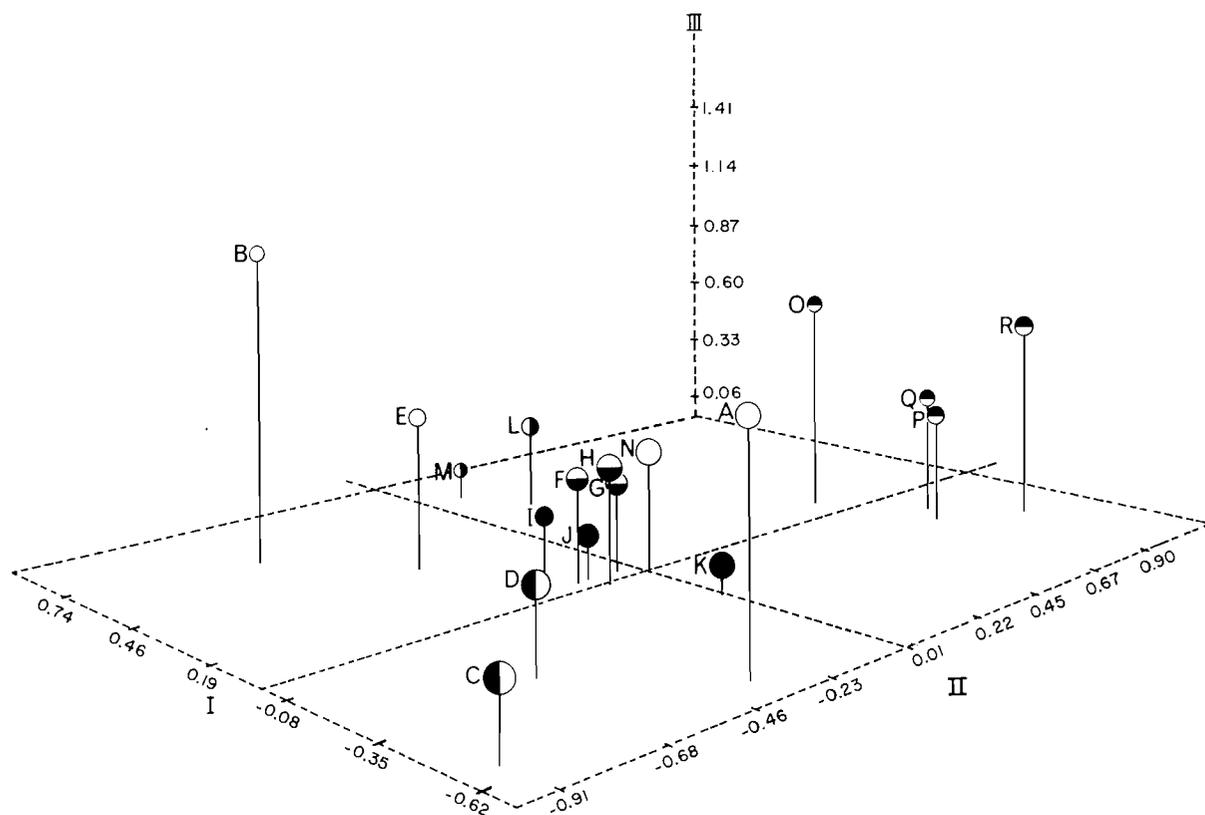


FIG. 5. Tridimensional model based on principal components analysis. The three axes represent the first three components. (A○) *F. purpurascens*, (B○) *F. argentina*, (E○) *F. cirrosa*, and (N○) *F. pampeana* are not included in any group. (C●) *F. tunicata* and (D●) *F. acanthophylla* (group 1). (F●) *F. monticola*, (G●) *F. thernarum*, and (H●) *F. scabriuscula* (group 2). (I●) *F. pallescens*, (J●) *F. p. var. scabra*, and (K●) *F. kurtziana* (group 3). (L●) *F. gracillima* and (M●) *F. ventanicola* (group 4). (O●) *F. contracta*, (P●) *F. magellanica*, (Q●) *F. pyrogea*, and (R●) *F. rubra var. simpliciuscula* (group 5).

four VChs. In the second component the contribution of the RChs is higher than in the other two (Table 3). Eight and nine characters of the first and second components, respectively, are quantitative and associated with the size of the reproductive and vegetative organs. This is not the case for the third component: only two quantitative characters occur in the first 10.

Figure 5 shows the relative distances among the OTUs based on the first three components. The model shows combinations of isolated and grouped taxa (Fig. 5). Complementary views of phenetic relationships were provided by CA at OTU-OTU taxonomic distances and OTU-OTU correlations. Two UPGMA phenograms were derived and a Consensus Program was used to test the degree of coincidence between the groups defined by each one of the phenograms (Fig. 6).

Five groups of closely related species emerged from the CP by comparing both phenograms in Fig. 6. They consist of *F. tunicata* and *F. acanthophylla* (group 1); *F. monticola*, *F. thernarum*, and *F. scabriuscula* (group 2); *F. pallescens*, *F. p. var. scabra*, and *F. kurtziana* (group 3); *F. gracillima* and *F. ventanicola* (group 4); *F. contracta*, *F. r. var. simpliciuscula*, *F. pyrogea*, and *F. magellanica* (group 5). *Festuca argentina*, *F. cirrosa*, *F. pampeana*, and *F. purpurascens* are not included in any of the five groups (Fig. 6). Group 5 appeared clearly separated from the rest, whereas the other four groups are relatively more similar to one another, especially in the phenogram based on taxonomic distances (Fig. 6A).

The phenogram based on the correlation coefficient shows a partial distortion with respect to that based on the taxonomic

distances (Fig. 6B). Sneath and Sokal (1973) suggested that the correlation coefficient gives relatively more emphasis to similarities in shape than in size. However, in these fescues size seems to be very important and the emphasis on shape might well produce a distortion in the phenetic relationships among the groups.

The combination of the relative position of the species given by the PCA tridimensional model and the arrangement of the taxa in groups detected by CA provides a better understanding of the phenetic relationships of the taxa analyzed (Fig. 5). Taxa of the first group are separated from the others by the first and second components (Fig. 5, C and D). Groups 2 (Fig. 5, F, G, and H) and 3 (Fig. 5, I, J, and K) are quite similar on components 1 and 2 and are only slightly separated by component 3.

Festuca pampeana, despite being very close to groups 2 and 3, does not belong to any of the former groups. This is due to the low contribution of the differentiating characters of *F. pampeana* to the first three components (Fig. 5, N). However, this taxon is separated from the rest by characters 23 and 41 (Table 1), which mostly contribute to the fifth component, and characters 5 and 6 (Table 1), to the sixth.

Festuca gracillima and *F. ventanicola* (group 4) are separated from the rest of the species by both the first and second component (Fig. 5, L and M).

The taxa included in group 5 are distantly related to the rest of the entities (Fig. 5, O, P, Q, and R). They can be arranged in subgroups representing two species closely related (*F. magellanica* and *F. pyrogea*, Fig. 5, Q and P) and two distantly

TABLE 2. Eigenvalues

Component	Eigenvalue	% total variation	Accumulative % variation
1	11.57	27.55	27.55
2	6.37	15.17	42.73
3	5.40	12.86	55.59
4	3.88	9.23	64.82
5	3.43	8.17	72.99
6	2.89	6.89	79.88

related taxa (*F. contracta* and *F. r. var. simpliciuscula*, Fig. 5, O and R). Coincidentally with CA, *F. purpurascens* and *F. argentina* are isolated and they do not belong to any of the groups (Fig. 5, A and B). Finally, *F. cirrosa* seems to be rather closer to groups 2 and 3, but the second and third components separate this species from groups 2 and 3 (Fig. 5, E).

Discussion

Vegetative vis-à-vis reproductive characters in Festuca

One of the interesting aspects in the genus *Festuca* concerning the vegetative characters is the taxonomic use of the internal morphology of the leaves. Following Hackel (1882), various authors (Saint-Yves 1927; Parodi 1953; Aiken et al. 1985) have used variation in the distribution of the sclerenchyma in the leaves for taxonomic purposes. In the species with no girders of sclerenchyma the variation in the distribution of the sclerenchyma bands within the specific range coincides with that observed by Connor (1960), Kjellqvist (1961), and Aiken et al. (1985). On the other hand lesser intraspecific variation in the anatomy of the leaves was observed in the species with bundles accompanied by girders of sclerenchyma. Although those observations restrict the taxonomic value of leaf anatomy in *Festuca*, nevertheless the analysis of cross sections of the leaves is useful. In the case of the Patagonian taxa the distribution of the sclerenchyma in the leaves not only helps to explain the geographical distribution of some of the species but also separates taxonomically the species of group 2 from those of group 3.

As far as the RChs are concerned, they have relatively more taxonomic weight than the VChs. The sizes of the inflorescence, spikelet, anther, glume, etc. are important for the taxonomy of the species examined here. On the other hand the PCA shows that characters such as hairs in the caryopsis in the Patagonian taxa seem to have a relatively low taxonomic weight, since all the taxa but two examined here have hairs in the tip of the ovary. In contrast this is one of the important characters for distinguishing the European species of *Festuca* (Hackel 1882).

Both VChs and RChs are complementary for a taxonomic classification of the Patagonian festucas and neither are enough if taken alone to define the phenetic relationships among the taxa. This is supported by the low degree of coincidence measured by the cophenetic correlation coefficient between the VChs matrix and that of RChs.

Taxonomic considerations, geographical distribution, and evolutionary relationships

Numerical analysis shows that the Patagonian fescues are a heterogeneous group of species phenetically related in different degrees. This is mainly a consequence of a reticulate combination of continuous and discontinuous vegetative and reproductive characters.

TABLE 3. Ten characters with the highest contribution to each of the components

Character	Contribution
First component	
(19) Shoot length	-0.88
(23) Panicle length	-0.81
(16) Presence of adaxial schlerenchyma	-0.80
(22) Shoot diameter at panicle base	-0.79
(12) No. of vascular bundles	-0.78
(37) Anther length	-0.77
(26) Spikelet length	-0.75
(27) No. of florets/spikelet	-0.75
(5) Blade length	-0.73
(13) Presence of schlerenchyma girders	-0.72
Second component	
(28) Length of the first floret	0.82
(31) Glume 1 length	0.69
(35) Length of the second internode of the spikelet	0.63
(26) Spikelet length	0.56
(30) Awn length	0.55
(6) Presence of anthocyanin in the sheath	-0.55
(42) Caryopsis length	0.54
(24) No. of spikelets/panicle	-0.54
(39) Lodicule length	0.51
(25) No. of nodes/panicle	-0.47
Third component	
(15) Continuous or discontinuous band of schlerenchyma under the abaxial epidermis	-0.69
(36) Rachilla scabrosity	-0.63
(40) Lodicule with marginal cilia	0.63
(9) Presence of a pulvinus glabrous or pubescent at the base of the lamina	-0.61
(29) Prickles and (or) hairs on the lemma	0.59
(17) Presence of short cells in the intercostal abaxial epidermis	-0.57
(38) Permanence of anthers on the mature caryopsis	0.52
(33) No. of nerves in glume 1	0.51
(42) Caryopsis length	-0.50
(18) Presence of stomata in abaxial epidermis	0.48

PCA and CA coincide showing that *F. purpurascens* is not related to any of the Patagonian taxa analyzed here: there is a clear gap between this species and the rest of the taxa with relatively more narrow leaves. *Festuca purpurascens* occurs in the humid open areas of the *Nothofagus* forests in the Patagonian Andes. It has extravaginal innovations which produce long rhizomes, broad leaves, large panicles with numerous spikelets, glumes with short awns, and densely pubescent ovaries. The presence of these characters suggests that these species could be considered the most primitive of the 18 taxa analyzed here.

As in the case of *F. purpurascens*, *F. argentina* and *F. pampeana* are not included in any of the five phenetic groups. The vegetative and reproductive characters suggest that these two taxa are not closely related to any of the Patagonian taxa examined. They seem to be allied to the species occurring from central and northern Argentina to Bolivia and Peru (Türpe 1969).

The leaf morphology, the structure of the inflorescence, the breeding system (cleistogamous) (Tallowin and Lewis Smith 1977), and the geographical distribution suggest that the taxa belonging to group 5 can be considered the most specialized taxa living in Patagonia. The species of this group are widely

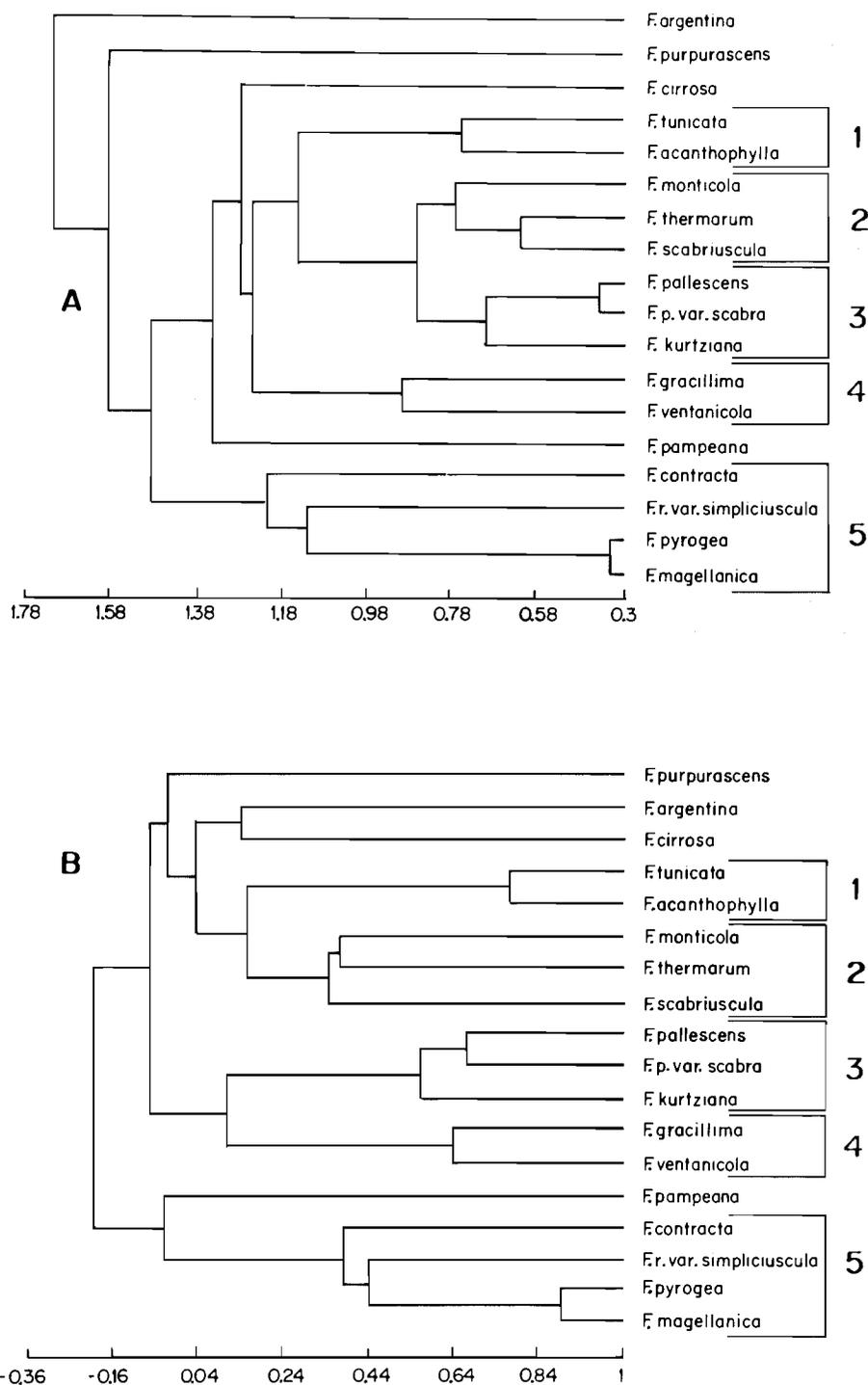


FIG. 6. Phenograms based on the vegetative and reproductive characters. (A) Taxonomic distance ($r = 0.81$); (B) correlation coefficient ($r = 0.80$). The groups were defined by Consensus Program (Strict).

spread along the Andes. *Festuca magellanica*, *F. pyrogea*, and *F. r. var. simpliciuscula* are widely distributed in the Patagonian Andes. These three taxa can be found from sea level in southern Patagonia to the high altitudes in the Andes at about 29° S. The morphological affinity among *F. magellanica*, *F. pyrogea*, and *F. r. var. simpliciuscula* suggests that these three taxa could be included in section *Oviniae* (Hackel 1882). Parodi (1953) included *F. magellanica* and *F. pyrogea* in *F. ovina* sensu lato.

The appearance of *F. contracta* in group 5 is a matter of

controversy since it has long glumes that almost cover the spikelets. It lives in extreme climatic conditions below 59° S in Tierra del Fuego Island, Iles de Kerguelen, Macquarie Island, South Georgia, and Falkland Islands (Islas Malvinas) (Moore 1983). Although the general aspect of this species is similar to those in group 5, the large glumes and the restricted geographical distribution suggest that *F. contracta* might well be classified under the subgenus *Helleria* proposed by Alexeev (1980).

In the alliance composed by the taxa belonging to groups 1,

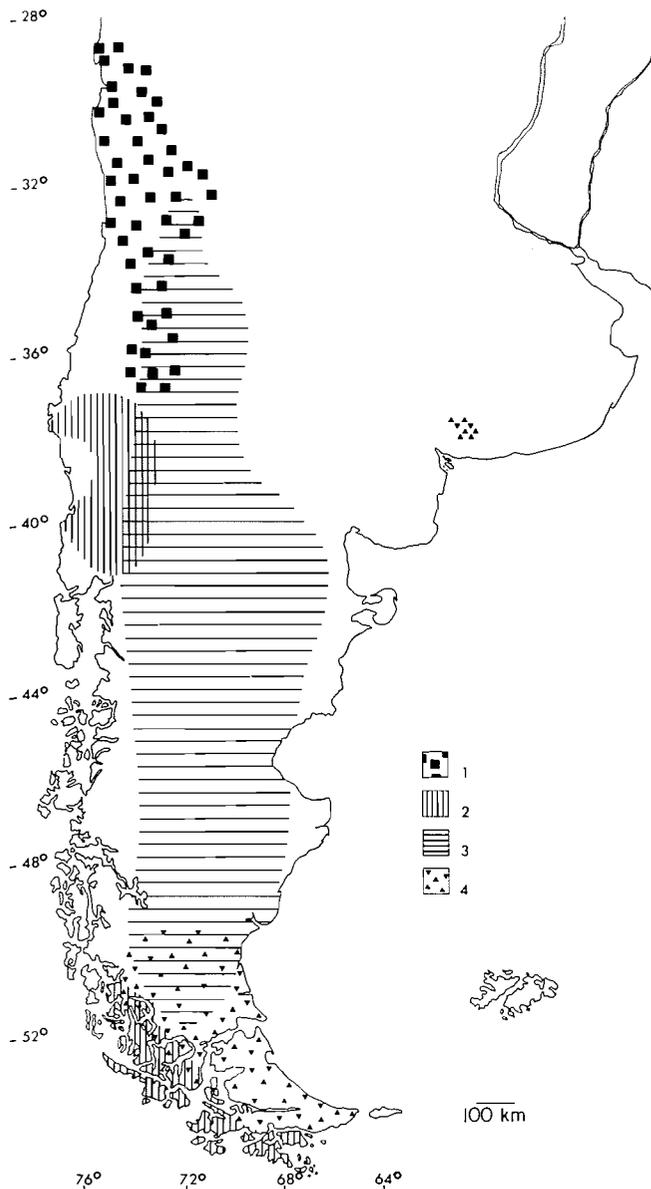


FIG. 7. Geographical distribution of the groups defined by cluster analysis. (Group 5 is not included to avoid an overlap with the rest of the groups.)

2, 3, and 4, *F. acanthophylla* and *F. tunicata* (group 1) are the only species examined that inhabit dry, warm regions. The abundant sclerenchyma tissue in their leaves is probably related to these climatic conditions.

Group 2 is composed of three taxa, although in the phenograms based either on VChs or on RChs, one of the three taxa is not included. The appearance of two species instead of three in the phenograms is due to the reduced number of characters, either vegetative or reproductive, considered. Although they have smaller leaves than those found in the taxa belonging to group 1, the sclerenchyma tissue in the three taxa is almost as abundant as in *F. acanthophylla* and *F. tunicata*. However, in contrast to these taxa the former are restricted to the humid regions of the Patagonian Andes (Fig. 7). The amount of sclerenchyma in the leaves might be fingerprints suggesting that these taxa once inhabited drier climatic conditions similar to those where the taxa of group 1 are living today.

The species without girders (groups 3 and 4) are widely

spread from regions with mesic to dry and cold climatic conditions (Fig. 7). This distribution coincides with a reduction in the sclerenchyma tissue together with progressive decrease in the leaf sizes. The ample adaptive ability found in *F. pallescens* is an example within the specific range of a significant variation in the size of the leaves related to different ecological conditions. The individuals inhabiting humid habitats have larger leaves than those living in steppes. The variation in leaf size also seems to be related to the geographical distribution of *F. pallescens*, which can be found as a dominant component of natural communities between 40 and 50° S. This species lives under different climatic conditions ranging from 25 to 1900 m above sea level and from 150 to 1065 mm of rainfall (Roig et al. 1985) and the individuals examined were sampled in these climatic ranges of variation (Fig. 7).

Festuca gracillima and *F. ventanicola* (group 4), despite of being phenetically similar, are geographically separated. *Festuca gracillima* inhabits dry cool regions of the Patagonian steppe between 50 and 55° S (Fig. 7). In contrast *F. ventanicola* lives in Sierra de la Ventana at 38° S, at 400 m above sea level (Fig. 7). *Festuca ventanicola* is not the only example of an endemic taxon of the former Sierras related to the Patagonian flora. There are other examples of endemic taxa related to that flora. The best known are various species of ferns (De la Sota 1967), which are evidence that in the past the Patagonian flora might have had a larger area of distribution on both sides of the Andes (Villagrán and Armesto 1980). This possibility may also be the explanation for *F. tunicata* living at 30° S but on the Pacific side of the Andes with other members of the Patagonian flora.

Although *F. cirrosa* is not included in any group, it seems to be related to the taxa belonging to group 2. However, it is excluded from this group by CA probably because of the large ligules and florets. This taxon is endemic to Tierra del Fuego (Moore 1983), living among gravels in the rocky beaches below 52° S.

The size, frequency of individuals, and number of different species living together are variable in the populations. Half of the taxa analyzed here appear scattered in diversified communities. The other half (*F. acanthophylla*, *F. gracillima*, *F. pampeana*, and the species belonging to groups 2 and 3) tend to be dominants in the communities examined. However, there are frequently areas where two related species are distributed in adjacent populations. The existence of hybrids in these areas cannot be discarded. On the other hand, sympatric populations with more than one species were only found when the taxa are distantly related.

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