ENVIRONMENTAL DETERMINANTS OF VEGETATION VARIATION ON TENERIFE (CANARY ISLANDS).

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Keywords: Environmental determinants, floristic and structure changes, altitudinal communities, Tenerife.

ABSTRACT:
The variation in structure and floristic composition of the vegetation of Tenerife and its relation to different environmental factors has been studied. With that aim 200 plots, stratified by altitude, wind-exposure, lithology, inclination and disturbance degree of the communities were located throughout the island. In each plot, the performances of the species present were assessed using density, cover and biovolume values. Resulting data were analized using the altitudinal distribution profiles of each species and cluster analyses.
Altitude, wind-exposure and, to a lesser degree, disturbance were found to be the major determinants of the vegetation variation, whereas lithology and inclination did not show high influence on it. The cluster analysis recognizes several communities in altitude, that have been delimited on a map of Tenerife.
Nomenclature: Hansen & Sunding, 1985.

INTRODUCTION:

Tenerife is the island within the Macaronesian region (Azores, Madeira, Canaries and Cape Verde) with the best conditions to carry out a study about the environmental determinants governing the variation in floristic composition and structure of the vegetation. These conditions are: i) its rather well conserved vegetation cover; ii) its developed altitudinal gradient; iii) its well defined slope types; iv) the lithological and chronological variability of its materials; v) its close net of meteorological stations and finally, vi) because it has been widely studied by many authors since Humboldt's stay on the island, almost 200 years ago.

The first analyses of the vegetation of Tenerife were carried out by Humboldt & Bonplandt (1814) and Buch (1819, 25) who recognized several altitudinal belts. In a later work, by Webb & Berthelot (1840), the wind-exposure was considered together with the altitude, as the principal factor of the vegetation distribution. During this century, the vegetation analyses were more centred in the description of single plant communities, although several studies borne an insular scope (cf. Pérez de Paz 1982). Floristic synopses, grouping the communities in vegetation belts, are due to Ceballos & Ortuño (1951) or to Wildpret & Arco (1987) or in bioclimatic belts to Rivas-Martínez (1983). In general, it can be concluded that there exists an agreement with respect to the distribution of vegetation according to altitudinal belts, but not to their number and precise limits.

The objectives of the present work have been: i) to elucidate which are the major environmental determinants of floristic and structural variation of the vegetation on Tenerife and ii) to determine which plant communities can be recognized on the island, as well as their distribution, floristic composition and ecological characterization.

STUDY AREA:

Tenerife is the largest island (2,058 km²) of the Canarian archipelago and of the Macaronesian biogeographical region. It has a triangle-based pyramid shape with a truncated apex at an altitude of 2,000 m in Las Cañadas, from which the volcano Teide, the highest peak of this region (3,718 m), rises. This well developed altitudinal gradient for an oceanic island is surpassed in the world only by Mauna Kea (4,205 m) and Mauna Loa (4,169 m), both hawaiian volcanoes. Its peculiar form, together with the predominating NE trade winds of our latitudes, has given rise to the establishment of two entirely different slope types: the N windward slope and the SE-SW leeward slope. At higher altitudes a third zone beyond the influence of the trade winds: the summit, can be distinguished.

Tenerife, like the other Macaronesian islands, is of volcanic origin; its oldest rocks (located on the Anaga and Teno massives, the NE and NW corners of the island, respectively) are estimated to be more than 7 millions years old (Carracedo 1984). Nevertheless, there is still volcanic activity with several eruptions during the last 500 years, the most recent (Volcán de Chinyero) in 1909. Both basaltic and phonolitic materials, corresponding to different vocanic cycles, can be found throughout the island.

The main environmental feature of Tenerife is caused by the existence of a thermic inversion separating a lower layer of humid, cool air from a higher layer of dry cold air at ca. 1200 m altitude. Due to this inversion the orographic ascension of moist air masses carried by the trade winds is prevented and leads to the acummulation of clouds below the inversion. This phenomenon, rather frequent on the windward slope of the island, is locally known as «mar de nubes» (cloud-sea). The altitudinal limits of this cloud-sea change throughout the year, reaching the highest elevation in winter (Huetz de Lemps 1969).

METHODS:

200 square plots with sides of 10 m were located throughout the island (Fig. 1) according to a stratified sample strategy. It was based on combina-

tions of several environmental classes defined according to altitude (belts of 100 m), wind-exposure (windward, leeward and summit), lithology type (basalts and phonolites) and age (younger and older than 10,000 years), floor inclination (0-15, 15-30 and 30-45°) and disturbance degree of the stand (less disturbed, moderately disturbed and highly disturbed). Thus, the vegetation existing on each combination of the environmental classes present on Tenerife was recorded by one plot. Nevertheless, in order to establish the importance of certain combinations covering large areas, more than one plot was asigned to them.

For each plot, the importance of the vascular plant species present was described using density (no. individuals/100 m^2), cover (%) and biovolume (cover x mean height of plant, expressed in m^3/100 m^2). Biomass (dry weight kg/100 m^2) was also assesed for plots with scrub-like vegetation using the alometric regressions provided for subdesert and high mountain species by Fernández-Palacios *et al* (1992) elsewhere. Community richness (no. sp./100 m^2) and diversity (using Shannon index) were also calculated for each plot. Finally, those species within the plot but bearing very low performances were included with a plus (+).

Table 1 provides an example of the description of the vegetation of some plots. All the data are available on request.

When the number of individuals of each species present in a plot was not too high, density was calculated by counting them; and cover with the product of the density times the mean individual area of the species (Fig. 2). However, if counting was impossible or unreliable, (e.g. too many individuals and/or very closely located) density was assessed via cover. The cover was calculated recording the vertical overlaps of the plants over 5 parallel straight lines 10 m long evenly distributed in the plot. Biovolume was estimated multiplying cover by mean plant height. All biometric measurements were averaged from 10 individuals per species within the plot selected by the nearest neighbour technique to a first one randomly chosen.

An univariate analysis of the altitudinal distribution of the more frequent species on Tenerife was carried out (Fig. 3). In order to contrast the significance of the vegetation belts multivariate methods were used. A global approach to the floristic and structural variation of vegetation and its correlation with the environment was obtained with the canonical correspondence analysis (CCA) included in the CANOCO ordination programmes package (ter Braak 1987).

A classification analysis of the floristic variation throughout the island was achieved using the hierarchical polythetic divisive method of TWINSPAN (Hill 1979). The division process was stopped for the whole set at the sixth division level or for each group when it included fewer than 20 plots. The end-groups obtained were ecologically characterized and mapped on Tenerife.

RESULTS:

Figure 3 represents the altitudinal profiles of some selected species among those with the highest frequency. It shows rather clearly the bell shaped curves which represented the different species which overlap along the gradient.

Figure 4 represents the biplot scores of the environmental variables introduced in the analysis. It is easy to observe the importance of altitude, positively correlated with the first ordination axis, and wind-exposure, negatively correlated with the second ordination axis. Disturbance degree of vegetation occupies an intermediate position, whereas neither lithology nor floor inclination, up to 45°, seem to be real significant factors of vegetation variation.

The hierarchical division of plant communities obtained by TWINSPAN is given in figure 5. Numbers represent preferential and non-preferential species for each group at each division, which are listed in Appendix 1. Finally, figure 6 gives the distribution of these 11 end-groups on a map of Tenerife.

DISCUSSION:

The rule of altitude and wind-exposure as major environmental determinants of the variation in Tenerife's vegetation, as stated in figure 4, was early recognized by the classical authors. Both are geographical factors with well known underlying climatic variation patterns.

Altitudinal changes suppose mainly changes in temperature (on Tenerife the mean annual temperature shifts from 21°C at the South coast up to some 2°C at the Teide Peak) and thus in frost events likelyhood and frequency. Furthermore, altitude variation implies changes in relative humidity and radiation values, and hence in evapotranspiration rates (Höllermann 1978; Leuschner & Schulte 1991). These features lead to the existence on Tenerife of a coast-summit thermic stress gradient, where the tolerance of the plant species to this kind of stress controls its distribution along the altitudinal gradient (Fernández-Palacios 1992).

On the other hand, variation in wind-exposure, at least in high islands within the trade winds influence, suppose changes in moisture and radiation. The existence on the NE windward slopes -including the local singularity existing on Ladera de Güímar at the South slope of the island (Figure 6)- of a woody heath and a cloud-forest is only possible to understand when the summer drought of the mediterranean clima of the Canaries is counteract with a local fog-drip effect owed to the cloud-sea (Höllermann 1981). Frequent and intense fog-drip effect, occurs locally along mountain crests and on wind-exposed sites, with a considerable ammount of fog precipitation (Kämmer 1974). Above and below the cloud-sea layer on the windward slope, vegetation suffers the existence of an hydric stress, that is stronger on the leeward slope, out of the cloud-sea influence, where the subdesert scrub is replaced in altitude by the pine forest.

The level of disturbance of the stand has been recognized as an intermediate determinant on Tenerife's vegetation variation. This is so because disturbance affects the vegetation variation model above recognized with two contradictory effects. On the one hand, disturbance has an homogenizer effect on vegetation, grouping together plots that belong to different altitudinal or wind-exposure classes, but sharing certain degree of disturbance as make evident the presence and performance of some generalistic species (such as *Opuntia ficus-barbarica, Cistus monspeliensis, Asphodelus aestivus, Aspalthium bituminosum*, etc.). This effect is due to the larger distribution amplitudes of the generalistic species when compared with specialistic ones (cf. Fig. 3). On the other hand, the different degree of disturbance shown by the plots, give rise to an effect that trends to separate them within the same altitudinal or wind-exposure class. Finally, it is also important to consider in this frame, the rareness of heavily disturbed areas at high altitudes (> 1,500 m) of the island.

Both lithological composition and age do not seem to play an important role in the variation of vegetation. Although it has been reported the existence of some species exclusively related to special lithologies, as phonolitic doms in the Canaries (Burchard, 1929), when the vegetation variation is analized with an insular scope, such events are unimportant. The age of the materials was supposed to be important because of the variations in the physic features of the stands owed to it, such as soil existence, porosity, nutrient availability, etc. Nevertheless, and very likely due to a wrong election of the border between young and old materials (10,000 years) non influence of it on vegetation variation was detected.

Finally, the inclination of the floor was found to be irelevant at least up to 45°. It is nonetheless a fact that when the slope is high enough, maybe more than 70°, it leads to the existence of special adapted soil-less cliff communities (Santos, 1983).

The bell-shaped curves showed in figure 3 by some of the more frequent species, as well as the fact that their centres of distribution seem to overlap along the altitudinal gradient, argues in favour of the continuous nature of vegetation variation (Whittaker, 1970).

Nevertheless, results of the divisive classification recognizes the existence of 11 types of communities (end-groups A-K) at the sixth level of division: peak vegetation, summit scrub, summit pine forest, pine forest, xeric heath, «monteverde», «jaral» (*Cistus* scrub), «tabaibal amargo» (*Euphorbia obtusifolia* scrub), «tabaibal-cardonal» (*Euphorbia balsamifera* + *E. canariensis* scrub), halophylous coastal belt and finally a vegetation complex of disturbed communities. All of them have been traditionally recognized, with the exception of the **summit pine forest**. This community is closely related to the summit scrub, due to the number of species shared, but is still bearing the presence of *Pinus* as landscape definer. The ecological characterization of these communities in terms of their tolerance to climatic stress and disturbance, as well as their indicator species, is given in table 2.

Figure 6 shows the TWINSPAN analysis end-groups delimited on a map of Tenerife. The limits between end-groups I and H have been omitted in order to simplify the map. It is easy to observe an altitudinal arrangement of the communities. The variation of the vegetation along altitudinal gradients has often be interpreted, as is the case for Tenerife too (Wildpret & Arco, 1987), as the existence of different altitudinal vegetation belts.

Apendix 1: List of plant species used as preferentials or non-preferentials in the TWINSPAN classification, as well as indicator species in the ecological characterization of the groups.

no.	species	no.	species
1	Adenocarpus foliolosus	26	Kleinia neriifolia
2	Adenocarpus viscosus	27	Launaea arborescens
3	Argyranthemum frutescens	28	Laurus azorica
4	Argyranthemum teneriffae	29	Lavandula canariensis
5	Artemisia thuscula	30	Micromeria varia
6	Aspalthium bituminosum	31	Myrica faya
7	Asphodelus aestivus	32	Neochamaelea pulverulenta
8	Carlina xeranthemoides	33	Nepeta teydea
9	Cenchrus ciliaris	34	Opuntia ficus-barbarica
10	Ceropegia fusca	35	Origanum vulgare
11	Chamaecytisus proliferus	36	Periploca laevigata
12	Cistus monspeliensis	37	Pinus canariensis
13	Cistus symphytifolius	38	Plocama pendula
14	Daphne gnidium	39	Pterocephalus lasiospermus
15	Descurainia bourgaeauana	40	Rubia fruticosa
16	Dittrichia viscosa	41	Rubus inermis
17	Erica arborea	42	Rumex lunaria
18	Euphorbia balsamifera	43	Schizogyne sericea
19	Euphorbia canariensis	44	Scrophularia glabrata
20	Euphorbia obtusifolia	45	Spartocytisus supranubius
21	Frankenia laevis	46	Tolpis webbii
22	Globularia salicina	47	Viburnum tinus
23	Hyparrhenia hirta	48	Visnea mocanera
24	Hypericum grandifolium	49	Viola cheiranthifolia
25	Ilex canariensis	50	Zygophyllum fontanesii

Table 1: Example of a vegetation inventories.

no. Locality / Especie	mean value / ind. diam. (m)	alt. (m)	dry w. (kg)	population value/ 100m² DENS. (ind)	COVER (%)	BIOV. (m³)	BIOM. (kg)
1 Roques de Fasnia							
Euphorbia balsamifera	1.25	0.64	1.09	25	30.50	19.41	27.17
Euphorbia canariensis	2.26	1.28	20.96	1	4.01	5.13	20.96
Schizogyne sericea	0.69	0.48	0.23	10	3.73	1.78	2.27
Launaea arborescens	0.68	0.45	0.24	8	2.90	1.30	1.95
Plocama pendula	1.06	0.38	0.21	4	3.55	1.33	0.85
Ceropegia fusca	0.29	0.45	0.11	3	0.20	0.09	0.34
Euphorbia obtusifolia	0.61	0.77	0.16	2	0.58	0.45	0.31
Hyparrhenia hirta				+			
Cenchrus ciliaris				+			
Community total				53	45.47	29.49	53.85
Richness / Diversity	9			2.18	1.65	1.60	1.57
11 Montaña Cobre							
Spartocytisus supranubius	4.38	1.55	58.00	2	36.14	56.02	139.21
Argyranthemum teneriffae	0.40	0.33	0.13	40	5.00	1.67	5.08
Descurainia bourgeauana	0.68	0.33	0.13	14	5.00	2.85	4.32
Scrophularia glabrata	0.60	0.55	0.47	4	1.25	0.69	1.90
Sideritis candicans	0.20	0.37	0.09	8	0.25	0.09	0.76
Pterocephalus lasiospermus	0.56	0.26	0.33	2	0.50	0.13	0.67
Andryala pinnatifida				+			
Tolpis webbi				+			
Community total				70	48.14	61.45	151.94
Richness / Diversity	8			1.84	1.25	0.58	0.58

Table 2) TWINSPAN end-groups ecological characterization.

End-group	indicator species	Ecological characterization
A	Viola cheiranthifolia	Peak vegetation. Viola communities of Teide peak, above 3,000 m altitude. Intense thermic (T <5°C with common frosts) and hydric (P < 300 mm, mainly as snow) stress.
B	Spartocytisus supranu. Descurainia bourgeaua. Adenocarpus viscosus Pterocephalus lasiosp.	Summit scrub. High-mountain cushion-like scrub communities between from ca. 2,100 m leeward and 2,000 m windward, up to 3,000 m. Dominated by Spartocytisus and growing under intense thermic (T 5-10°C with likely frost as well as wide daily thermic amplitude) and moderate hydric (P ca 500 mm, mainly as snow) stress.
C	Pinus canariensis Chamaecytisus prolife. Carlina xeranthemoides Pterocephalus lasiosp. Adenocarpus viscosus	Summit pine forest. Open and low forest (canopy ca 10 m) dominated by Pinus with common elements of the summit scrub, extending above ca 1,800 m on both slopes up to the timberline. Subject to lighter climatic conditions than the summit scrub, but still prone to frost.
D	Pinus canariensis Chamaecytisus prolife. Adenocarpus foliolosus Cistus monspeliensis Erica arborea	Pine forest. Tall forest (canopy ca 30 m) dominated by Pinus growing on both slopes below 1,800 m down to ca 1,300 at windward and ca 700 m at leeward. Subject to moderate thermic stress, with possible frost. Subject to a high variability of precipitation, the windward pine forest is humid, and the leeward one drier. It is an oligospecific community bearing the highest biomass of the island.
E	Ilex canariensis Erica arborea Cistus monspeliensis Cistus symphytifolius	Xeric Erica-Myrica heath. Singular community closely related to the unique windward zone of the South slope (Ladera de Güímar) with the characteristic elements of the normal heath -included in "monteverde" such as Erica, Myrica or Ilex, plus other species with xeric affinities like both Cistus species.

F	Ilex canariensis Laurus azorica Myrica faya Erica arborea Daphne gnidium	"Monteverde" belt, including both laurel forest and Erica-Myrica woody heath ("fayal-brezal"). Closely related to windward midlands (ca 600-1200 m) the contact zone of the cloud sea, due to the NE trade winds. These communities grow under suitable conditions (T 13-15°C and P> 1,000 mm + fog-drip), and are thus not subject to any climatic stress. Zone with highest Neto Primary Production of the island.
G	Cistus monspeliensis Chamaecytisus prolife. Aspalthium bituminosum	"Jaral". Immature scrub community dominated by the mediterranean Cistus monspeliensis, distributed at different altitudes on both slopes constitutes a disturbed phase of the potential pine forest.
H	Opuntia ficus-barbarica Euphorbia obtusifolia Cistus monspeliensis Kleinia neriifolia Artemisia thuscula	Vegetation complex of disturbed communities constituting transitional communities between "jarales" (end-group G) and "tabaibales amargos" (end-group H). Distributed largely on leeward slopes close to urban areas.
I	Euphorbia obtusifolia Opuntia ficus-barbarica Periploca laevigata Artemisia thuscula	"Tabaibal amargo". Disturbed phase of the sub-desert coastal scrub, with Opuntia and Euphorbia obtusifolia dominant. Present on both slopes.
J	Euphorbia balsamifera Euphorbia canariensis Plocama pendula Launaea arborescens	"Tabaibal-cardonal". Sub-desert coastal scrub, dominated by Euphorbia balsamifera and E. canariensis occupying the low zones of windward (up to 300 m) and leeward (up to 600 m) slopes. Prone to intense hydric stress (P <250 mm in less than 15 rainy days per year) and bearing the highest values of species richness of the island.
K	Frankenia laevis Euphorbia balsamifera Schizogyne sericea	Halophylous coastal belt. Scattered low scrub community related to the sea, and thus distributed at sea level around the island and subject to high salt stress as well as the zonal hydric stress.

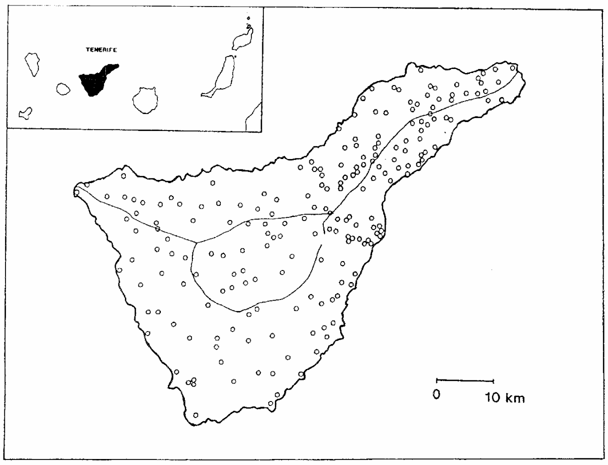


Figure 1: Location of the 200 sample plots throughout the island.

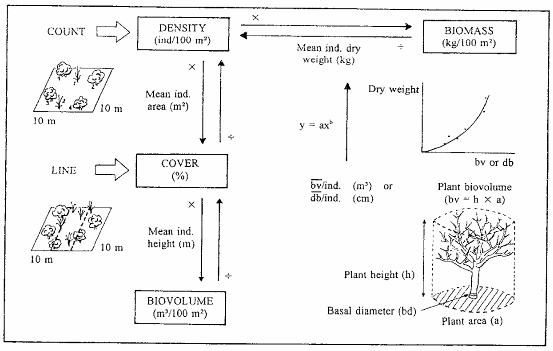


Figure 2: Scheme of the data collection strategy followed during the field work.

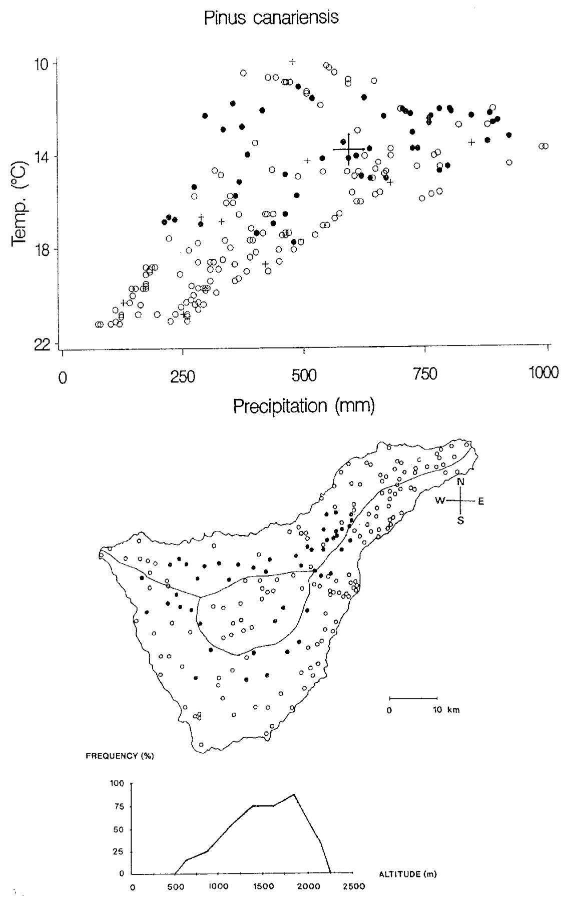
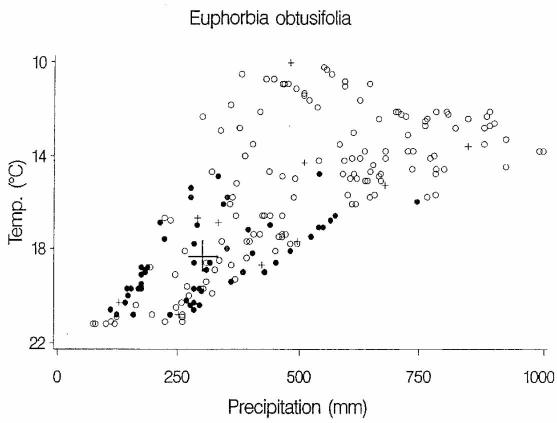
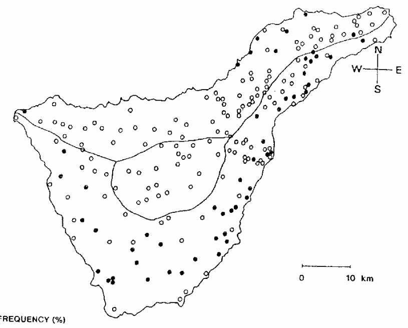
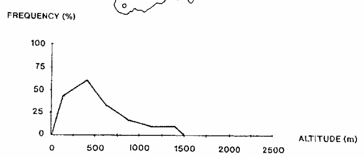


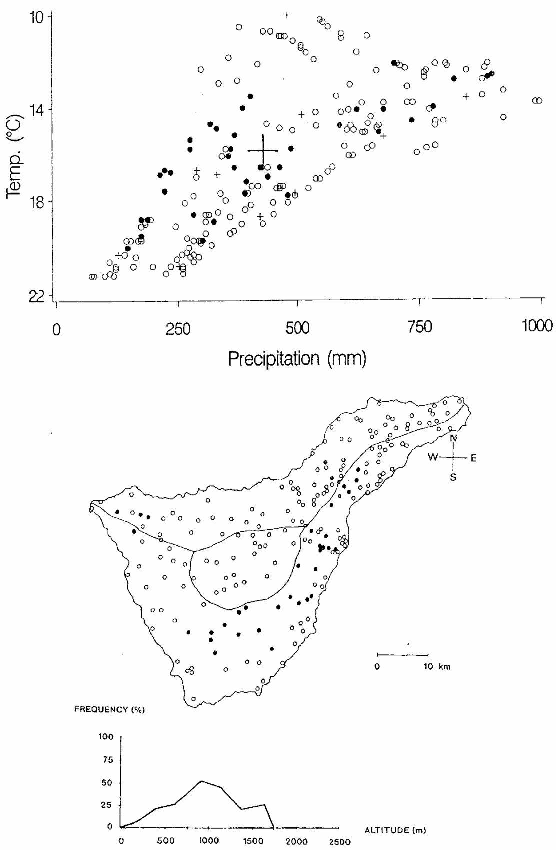
Figure 3: Altitudinal distribution of some of the more frequent plant species on Tenerife.

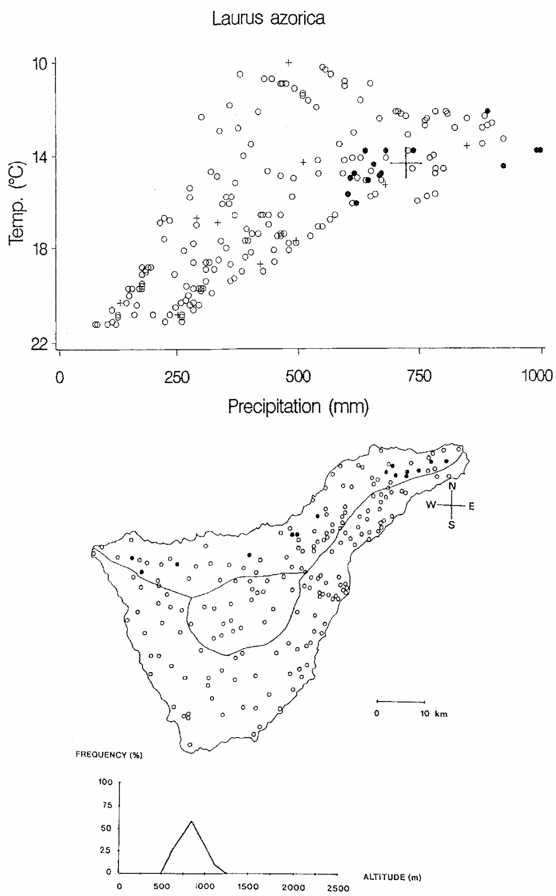

Euphorbia obtusifolia
10
14
18
22
Temp. (ºC)
0
250
500
750
1000
Precipitation (mm)


N
W
E
S
0
10 km

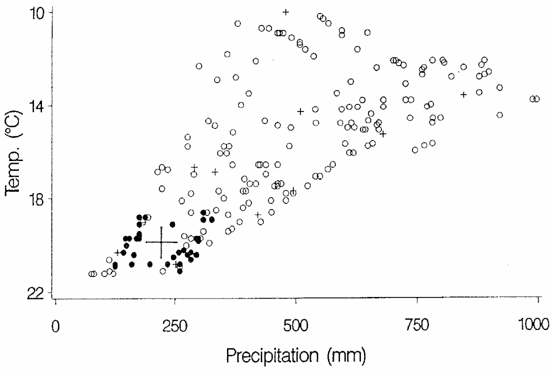

FREQUENCY (%)
100
75
50
25
0
0
500
1000
1500
2000
2500
ALTITUDE (m)

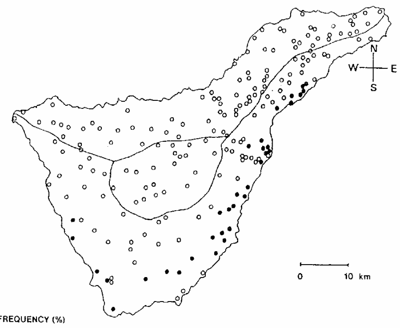
Cistus monspeliensis

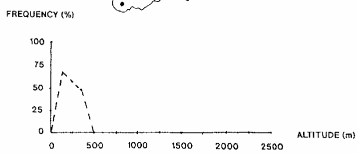



Laurus azorica
Temp. (°C)
10
14
18
22
0
250
500
750
1000
Precipitation (mm)
N
W
E
S
0
10 km
FREQUENCY (%)
100
75
50
25
0
0
500
1000
1500
2000
2500
ALTITUDE (m)

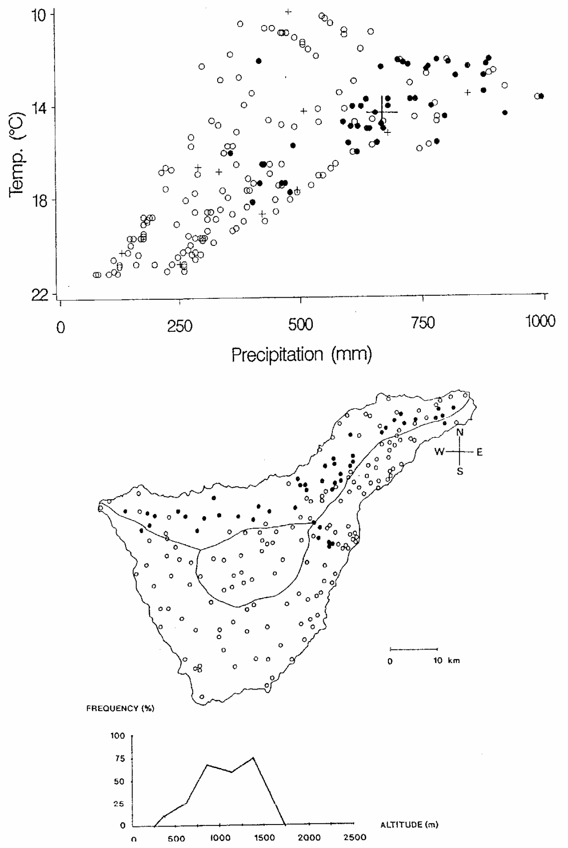
Plocama pendula

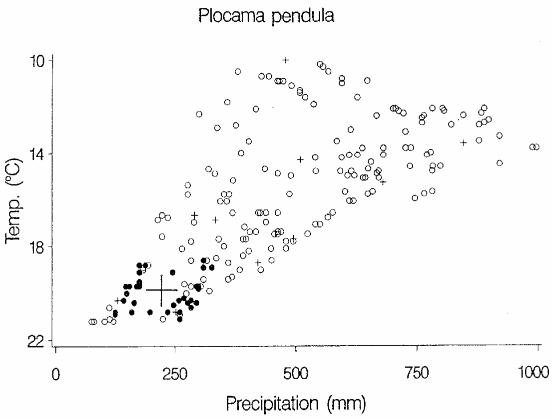


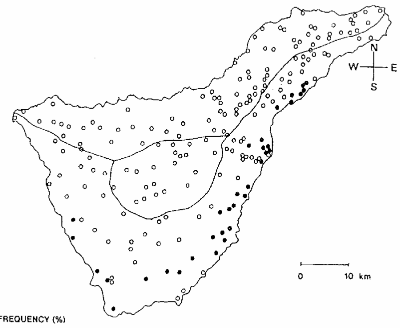


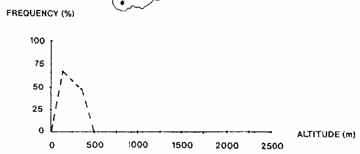


Erica arborea




Plocama pendula
Temp. (°C)
10
14
18
22
0
250
500
750
1000
Precipitation (mm)


N
W
E
S
0
10 km


FREQUENCY (%)
100
75
50
25
0
0
500
1000
1500
2000
2500
ALTITUDE (m)

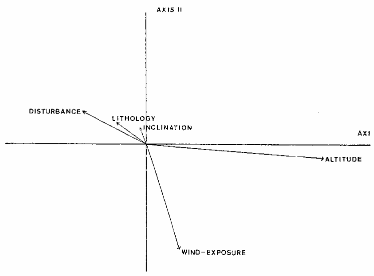


Figure 4: Biplot scores of the environmental variables introduced in the canonical correspondence analysis (CCA).

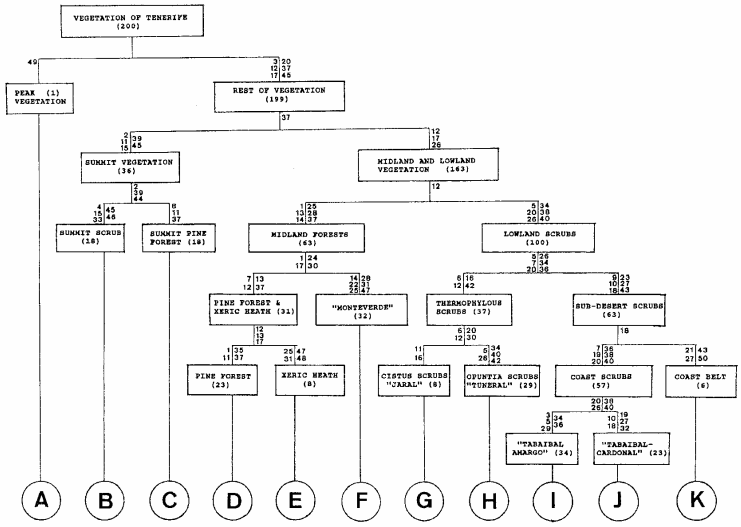


Figure 5: Hierarchical division of the plant communities obtained by TWINSPAN. Numbers referring to preferential and non-preferential species are listed in Appendix 1. Number of plots included in each group are given in brackets.

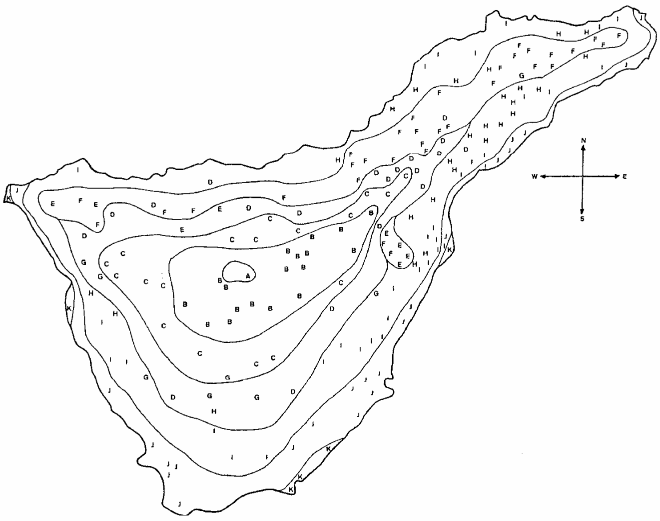


Figure 6: Distribution of the eleven end-groups recognized by TWINSPAN on Tenerife. Limits between end-groups H and I have been ommited to simplify the map.

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