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Climatic responses of plant species on Tenerife, The Canary Islands

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Abstract. The distribution of 44 common vascular plant species on Tenerife, The Canary Islands, has been related to the variation in temperature and precipitation. Frequency values for these speceis were obtained using a stratified sampling system with 200 10 m × 10 m plots distributed all over the island. A model is proposed relating variation in vegetation to altitude according to two main climatic gradients occurring between the 3718 m summit and the coastline of Tenerife. The vascular plants have been classified into guilds according to their presumed tolerance to cold and drought; one remainder group includes species which are randomly distributed without any relation to climatic variation. Differences between the guild structure suggested here and common knowledge of plant species occurrence in the well-known vegetation belts of Tenerife are explained by assuming disturbance and local ground-water availability as additional decisive factors.

Keywords: Altitudinal variation; Cold tolerance; Drought tolerance; Gradient; Guild.

Nomenclature: Hansen & Sunding (1985).

Introduction

Recently, theoretical models have been developed for the explanation and classification of strategies amongst plant species. The linear r / K selection model of MacArthur & Wilson (1967), which can be seen as an expression of responses to disturbance, was a starting point. It has been widely accepted and used as a basis for more elaborate models in which a dimension of environmental adversity is added (e.g. Whittaker 1975; Southwood 1977; Greenslade 1983). Adversity is now generally referred to as stress (Grime 1977) or impoverishment (Taylor, Aarssen & Loehle 1990; see Oksanen & Ranta 1992 for a general discussion). Essential factors in the stress complex are those reducing the carrying capacity of the ecosystem, such as length of the growing season, temperature, precipitation and nutrient availability. Grime's 'triangle', C-S-R- model with the Competitive, Stress-tolerant and Ruderal strategies differs from habitat templet models in the number of viable strategies recognized and the importance assigned to competition (Oksanen & Ranta 1992).

Tenerife has a well-known flora and vegetation (e.g. Pérez de Paz 1982), an extremely well-developed altitudinal gradient and a dense net of meteorological observations. Thus, it can be used as a test case for the analysis of such models, especially regarding temperature and precipitation as stress factors, i.e. cold and drought.

In a previous study altitude and wind-exposure, both highly correlated with temperature and precipitation, were found to be the main environmental factors that explain variation in floristic composition and structure in the vegetation of Tenerife (Fernández-Palacios 1987). On the other hand, the mineral composition, and hence nutrient availability, of the soils do not vary much due to their homogeneous volcanic origin (Fernández-Caldas, Tejedor & Quantin 1985). Thus, a two-dimensional environmental space with temperature and precipitation as axes would be a useful model to explain the spatial distribution and niche structure of the main plant species constituting the vegetation of Tenerife.

Study area

Tenerife, 2058 km^2, is the largest island of the Canary archipelago and of Macaronesia at large. It has a triangle-based pyramid shape with a truncated apex at 2000 m a.s.l. at Las Cañadas, from which the volcano Teide rises with a peak reaching 3718 m, the highest in Macaronesia. This peculiar form, together with the predominating northeastern trade winds, has brought about a striking contrast between the northern windward slope and the southeastern to southwestern leeward slope of the island. At higher altitudes a third zone beyond the influence of the tradewinds, can be distinguished.

Tenerife is of volcanic origin, as are the other Macaronesian islands; its oldest rocks (in the Anaga and Teno massives) have an estimated age of > 7 million yr (Carracedo 1984). Volcanos are still active with several eruptions during the last 500 yr, the most recent one dating from 1908 (Volcán de Chinyero).

The main environmental differentiation on Tenerife is caused by the existence of a temperature inversion

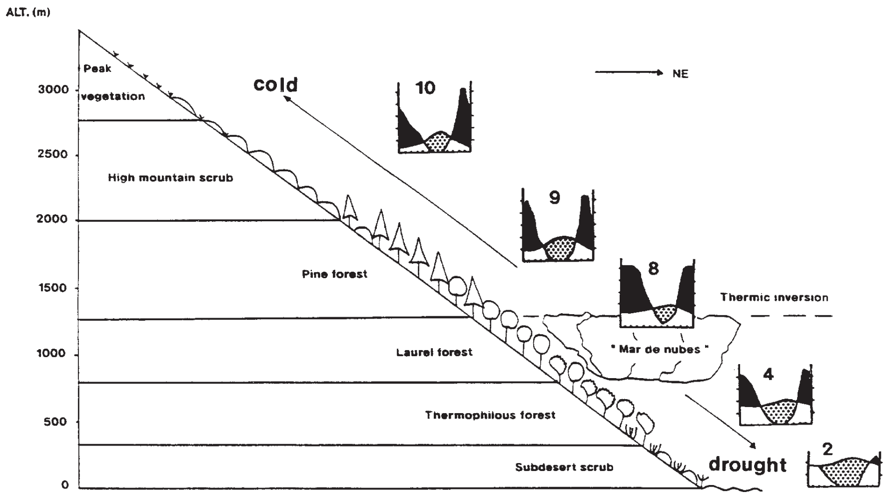

Fig. 1. Vegetation belts on the northeast slope of Tenerife, showing the altitudinal extension of the 'cloud sea' zone (mar de nubes) and the temperature and precipitation gradients. Simplified climate diagrams are added; the numbers refer to meteorological stations mentioned in Table 1.

separating the lower layer of humid, cool air from a higher layer of dry cold air at ca. 1200 m a.s.l. Due to this inversion the lift of moist air masses carried by the trade winds is prevented and leads to the accumulation of clouds below the inversion. This phenomenon, rather usual on the windward slope of the island, is locally known as 'mar de nubes' (cloud sea). The altitudinal limits of this cloud sea change during the year, reaching their highest elevation in winter (Font Tullot 1955).

Climatic gradients on Tenerife

My approach to the climatic gradients found on Tenerife, and also on other Canary islands, is as follows: the 'cloud sea' environment at 600 - 1200 m provides optimal conditions for plant growth, lacking any kind of climatic adversity, with a mean annual temperature between 13 - 15 °C, an annual precipitation > 700 mm and no frost or summer drought (Gandullo 1991). In either direction away from this zone a gradient appears, one of decreasing temperature upwards, implying cold stress, and one of decreasing moisture downwards, implying drought stress (Fig. 1, Table 1).

The decrease in temperature goes as far as to an annual mean close to 0 °C at the peak of the Teide (Sánchez Mejías pers. comm.). The main damage to plants related to low temperatures is the formation of extracellular ice (Fitter & Hay 1987) which occurs in those zones of the island where frost is frequent during winter, from ca. 1500 m upwards. The frost-free period at Vilaflor, at 1450 m, is still 333 days, but at Izaña, at 2350 m, it is only 149 days.

Although maximum temperatures on the island seldom exceed 40 °C (this under the influence of Saharian winds), the mean maximum temperature of the warmest month is ca. 30 °C, implying the absence of stress caused by high temperatures (Larcher 1983; Fitter & Hay 1987).

On the other hand, precipitation decreases drastically towards the coast, reaching its lowest level at the southeastern and southwestern coastal zones, with < 200 mm/yr below 300 m a.s.l. Moreover, most of this rainfall comes with infrequent Atlantic storms, so that the number of rainy days here is < 20/yr (Marzol 1984). Only xerophytic species can stand this drought adversity.

Forests, the communities with the highest carrying capacity (biomass and net primary production) occurring on Tenerife (Fernández-Palacios et al. in press), are found only in or near the cloud-sea zone. Laurel forests and the 'fayal-brezal' (*Erica arborea-Myrica faya* forest) occur right in the middle of this zone, thermophilous forest immediately below, and pine forest (*Pinus canariensis*) immediately above. Shrubland dominates both above and below the forest belt, where environmental adversity reduces the carrying capacity. At the

Table 1. Meteorological stations on Tenerife used in this study, with data on altitude, Alt (m), slope, Sl (°), mean annual temperature, Ta (°C), mean minimum temperature of the coldest month, Tc (°C), annual precipitation, Pa (mm) and summer (June - August) precipitation, Ps (mm); - means: no data vailable. The numbers of the stations are the same as in Figs. 1 and 2.

No	Station	Alt	Sl	Ta	Tc	Pa	Ps
1	Faro de Rasca	20	S	20.3	-	129	-
2	Santa Cruz	37	SE	20.8	14.3	252	0
3	Icod	230	N	18.7	11.4	421	12
4	Tacoronte	450	N	17.7	-	495	-
5	Granadilla	550	SE	16.9	-	290	-
6	Tamaimo	600	SW	16.9	-	332	-
7	Los Rodeos	640	N	15.3	8.2	680	28
8	Aguamansa	1150	N	13.7	4.7	510	3
9	Vilaflor	1500	SE	14.3	4.7	510	3
10	Izaña	2350	C	9.8	0.8	480	4

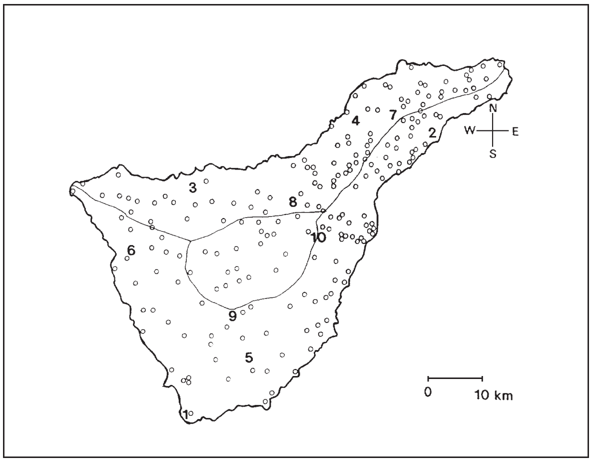

Fig. 2. Distribution of 200 sampling plots over Tenerife (open circles) and location of meteorological stations (dots). Numbers are the same as in Table 1.

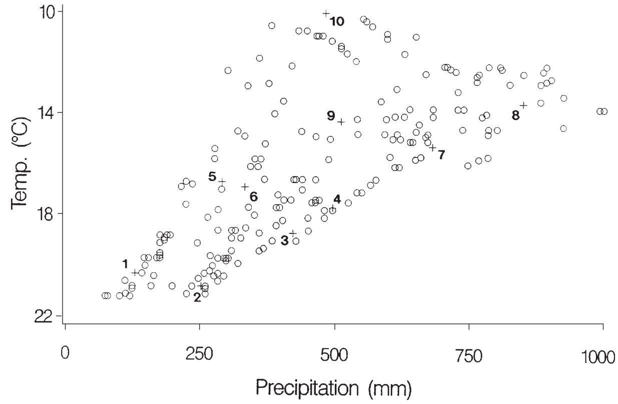

Fig. 3. Distribution of sampling plots and meteorological stations (see Fig. 2) in the climatic space.

extremes of the gradients we find drought-adapted semi-desert and high-mountain cold-adapted shrubland and alpine vegetation respectively (Fig. 1).

Methods

200 10 m × 10 m plots were laid out over the island (Fig. 2) following a stratified sampling strategy representing variation in altitude, exposition, degree of disturbance, composition, age of bedrock and inclination. Presence-absence data for 258 vascular plant species were recorded; the 44 species with a frequency > 6 % (the lowest value allowing a Chi-square test), were used in the present analysis. Species distribution maps (App. 1) were made (cf. Voggenreiter 1974; Barquín & Voggenreiter 1987), and altitudinal distribution patterns for the N and S slopes of the island were derived from frequency values over plots at 250-m intervals.

Climate data recorded by the ‘lnstituto Nacional de Meteorología’ at 179 meteorological (47 thermo-pluviometric and 132 pluviometric) stations located on Tenerife were used to calculate regressions of mean annual temperature and annual precipitation with altitude (Ferrer 1989). Different temperature regression equations were calculated for N and S slopes, and different regressions for precipitation were used in each of the regions distinguished as to exposition. These regressions were used to estimate climatic characteristics for all 200 plots.

The first step in the analysis was to decide if the distribution patterns shown by the species were due to stochastic or deterministic events. Therefore a Chi-square test (at p = 0.05) for species distributions was applied along each climatic gradient in order to assess significant distribution patterns.

Significant distribution patterns of species may be largely due to the climatic factors analysed. In order to evaluate the response of those species to both climatic factors, a normal distribution of its performance along the climatic gradient is assumed (Whittaker 1970). The centre of distribution of the bell-shaped curve is given by the average of the mean annual temperatures (°C) or annual precipitation values (mm) of those plots where the species was present, while the distribution amplitude is given by the range of the temperature or precipitation values (Table 2). However, as the data represent only a small part of the populations involved, the real amplitude of the species distribution along the gradients is expected to be somewhat larger.

To characterise each species response, two different parameters of the distribution are needed: (1) for the level of tolerance of cold and drought adversity, for which I have used the lowest values of the mean annual temperature or precipitation where the species was recorded; (2) for the amplitude of distribution along both gradients, for which I took the range of the data for each species. Finally, as a basis for the climatic characterisation of the species, a precipitation-temperature diagram was constructed with the position of the 200 plots, and of 10 meteorological stations all over the island (Fig. 3 and Table 1). The climatic response of each of these species was expressed by the centroid of its distribution and by the degree of scatter in the cloud of points in that diagram.

Results

A list of the 44 species included in the analysis, their frequency values (%), life form (Raunkiaer 1934) and chorological status (Lems 1960) is presented in Table 2.

Table 2. Characteristics of 44 frequent plant species on Tenerife. Cg = Climatic guild; for symbols, see Table 3 and Text. No. = Frequency ranking; Fr = frequency (%); Lf = life form according to Raunkiaer; Cs = chorological status according to Lems: En = Canary or Macaronesian endemic; Na = native; In = introduced; T-m, T-range = Temperature mean, range; P-m, P-range = Precipitation mean, range.

Cg	Species	No.	Fr	Lf	Cs	T-m	T-range	P-m	P-range
Ab	*Pinus canariensis*	3	25.5	M	En	13.9	11.1 - 17.8	599	217 - 932
Ab	*Pterocephalus lasiospermum*	36	8.0	Ch	En	12.1	10.3 - 14.7	561	463 - 805
Ab	*Andryalla pinnatifida*	37	7.5	Ch	En	14.5	10.9 - 18.2	645	401 - 880
Ai	*Aspaltium bituminosum*	9	18.5	Ch	Na	17.2	10.8 - 20.6	446	111 - 780
Ai	*Chamaecytisus proliferus*	16	15.5	M	En	13.8	10.8 - 18.8	545	175 - 900
Ai	*Adenocarpus viscosus*	29	9.0	N	En	12.5	10.3 - 15.4	500	276 - 848
Ai	*Spartocytisus supranubius**	31	8.5	N	En	10.9	10.2 - 11.9	510	379 - 648
Ba	*Euphorbia obtusifolia*	1	27.0	N	En	18.5	14.8 - 20.8	309	111 - 746
Ba	*Asphodelus aestivus*	7	21.5	G	Na	17.5	12.4 - 20.8	357	111 - 900
Ba	*Argyranthemum frutescens*	10	17.5	Ch	En	18.8	14.6 - 20.8	330	111 - 736
Ba	*Micromeria hyssopifolia*	22	13.0	Ch	En	18.3	14.9 - 20.4	273	146 - 438
Ba	*Scilla haemorrhoidalis*	33	8.5	G	En	18.9	14.8 - 20.8	293	111 - 541
Bb	*Erica arborea*	4	24.5	M	Na	14.5	12.1 - 18.6	674	356 - 998
Bb	*Daphnea gnidium*	20	13.0	N	Na	14.3	12.1 - 17.4	686	356 - 932
Bb	*Myrica faya*	21	13.0	M	Na	14.1	12.1 - 17.4	710	417 - 998
Bb	*Ilex canariensis*	23	12.5	M	En	14.3	12.1 - 17.4	706	417 - 998
Bb	*Adenocarpus foliolosus*	40	7.5	N	En	14.1	12.1 - 17.8	745	375 - 998
Bc	*Origanum virens*	35	8.0	Hc	Na	13.5	12.1 - 15.7	747	606 - 923
Bc	*Laurus azorica*	39	7.5	M	En	14.4	12.1 - 16.1	729	565 - 998
Bi	*Cistus symphytifolius*	19	14.0	N	En	14.4	12.1 - 17.8	549	235 - 880
Ca	*Hyparrhenia hirta*	2	27.0	Hc	Na	19.0	15.8 - 21.1	290	111 - 549
Ca	*Kleinia neriifolia*	5	23.5	N	En	18.4	15.8 - 20.8	338	124 - 746
Ca	*Plocama pendula*	11	17.0	N	En	20.0	18.6 - 21.1	224	124 - 325
Ca	*Rubia fruticosa*	12	16.0	N	En	18.4	15.8 - 21.1	368	169 - 575
Ca	*Opuntia ficus-barbarica*	13	16.0	S	In	18.1	15.8 - 19.8	376	154 - 746
Ca	*Launaea arborescens*	15	16.0	Ch	En	20.2	18.6 - 21.2	196	074 - 308
Ca	*Periploca laevigata*	17	14.5	L	Na	18.6	15.8 - 21.1	334	111 - 575
Ca	*Euphorbia balsamifera*	18	14.5	N	En	20.1	18.1 - 21.2	221	079 - 450
Ca	*Euphorbia canariensis*	24	11.5	S	En	19.6	17.1 - 21.2	248	079 - 540
Ca	*Lavandula multifida*	25	10.0	Ch	En	19.2	16.9 - 21.1	273	124 - 449
Ca	*Cenchrus ciliaris*	26	10.0	Hc	Na	15.9	12. - 19.4	610	142 - 450
Ca	*Schizogyne sericea*	32	8.5	N	En	20.4	18.8 - 21.2	187	074 - 308
Ca	*Ceropegia fusca*	42	7.0	S	En	19.8	18.6 - 20.8	195	142 - 308
Cb	*Rumex lunaria*	38	7.5	N	En	17.8	15.8 - 20.0	411	205 - 880
Ci	*Pallenis spinosa*	34	8.5	Th	In	18.6	16.0 - 21.1	350	142 - 746
Ci	*Artemisia thuscula*	14	16.0	N	En	18.1	15.7 - 20.4	419	146 - 783
Ia	*Cistus monspeliensis*	8	19.5	N	Na	16.1	12.1 - 20.0	432	148 - 900
Ib	*Viburnum rigidum*	43	7.0	M	En	14.9	12.1 - 17.4	649	417 - 990
Ic	*Hypericum grandifolium*	41	7.0	M	En	13.8	11.6 - 16.1	703	614 - 891
Ii	*Micromeria varia*	6	22.0	Ch	En	15.7	12.1 - 19.0	550	183 - 998
Ii	*Rubus inermis*	27	9.5	Th	In	17.3	13.8 - 20.6	477	359 - 998
Ii	*Anagallis arvensis*	28	9.0	Th	In	17.3	13.8 - 20.6	477	111 - 681
Ii	*Dittrichia viscosa*	30	8.5	N	Na	16.9	14.1 - 20.0	478	175 - 772
Ii	*Globularia salicina*	44	6.5	N	En	16.0	12.4 - 18.2	590	390 - 923

*The lower limit of the temperature range for this species is probably lower, but no data from above 2400 m are available. The species was found in the two plots at the highest altitudes, at 2900 and 3100 m.

Species tolerance to low temperatures was related to frost risk, considered as a limiting growth factor (Klaus & Frankenberg 1979; Rivas Martínez 1983; Hill, Read & Busby 1988; for a review see Tuhkanen 1980). The mean minimum temperature of the coldest month is a better parameter to describe the probability of frost events, but this parameter is available only for a few stations on Tenerife. On the other hand, it should be closely correlated to the mean annual temperature (based on data from six stations on Tenerife: $r = 0.913$, $p < 0.01$; cf. Table 1).

Thus, a preliminary classification of species tolerances to cold and drought was attempted, using a two-letter combination. For cold the lowest mean annual temperature where the species was present (t) was used:

A. Cold tolerant: $t < 12$ °C (frost most probable).
B. Moderately cold tolerant: t 12-15 °C (frost possible).
C. Cold intolerant: $t > 12$ °C (frost-free).
I. Indifferent: random distribution.

For drought tolerance a similar approach was used. The limiting factor on the Canary Islands, having a mediterranean-type climate, seems to be the amount of summer (June - August) precipitation (Rivas Martínez 1983). Summer precipitation is very low all over the island (cf. Table 1) and it is correlated with annual precipitation. Fog drip (horizontal precipitation) may be an important compensating factor for species living inside the cloud zone (Ceballos & Ortuño 1951; Kämmer 1974), but there are only preliminary and partially con-

Table 3. Climatic guilds based on cold and drought tolerance for 44 frequent plant species on Tenerife. Number of species in each guild in brackets.

	Temperature (°C)			
	< 12	12 - 15	> 15	Indifferent
Precipitation (mm/yr)				
< 200	Aa (-)	Ba (5)	Ca (13)	Ia (1)
200 - 500	Ab (3)	Bb (5)	Cb (1)	Ib (1)
> 500	Ac (-)	Bc (2)	Cc (-)	Ic (1)
Indifferent	Ai (4)	Bi (1)	Ci (2)	Ii (5)

tradictory data available. Thus, using the lowest precipitation value (*p*) where the species was collected, the following classification of tolerance of drought is proposed:

a. Drought tolerant: $p < 200$ mm.
b. Moderately drought tolerant: $p = 200 - 500$ mm.
c. Drought intolerant: $p > 500$ mm.
i. Indifferent: random distribution.

Table 3 shows a preliminary classification resulting from an analysis of the most frequent species on Tenerife according to their climatic tolerances. Each combination is formed by species with similar responses to cold and drought adversity. Species having a similar combination of ranges can be considered to form a plant guild (cf. van der Maarel 1988).

Discussion

From the combinations of possible tolerances , three of them are not represented by any of the most frequent species on Tenerife. These are Cold-Drought tolerance (Aa), Cold tolerance-drought intolerance (Ac) and Cold intolerance - drought intolerance (Cc). The first combination may occur only high up the Teide at > 3000 m, but we have no records to confirm the expected decrease of precipitation there (Sánchez Mejías pers. comm.). Some infrequent species on Tenerife, such as *Viola cheiranthifolia*, could be Aa because of their restricted distribution on the Teide peak.

Species of the Ac type are probably absent on Tenerife as a whole. The absence of cold-drought intolerant, Cc, representatives amongst the most frequent species, is probably due to the poor representation of zones with such characteristics (windward ravines inside the 'cloud sea'). Infrequent tree species of the *Lauraceae* such as *Persea indica* and *Ocotea foetens* occurring in such habitats, may be representatives of this type.

The high number of species (13) of the Ca group is probably due to the high proportion of the island's area having high temperatures and low precipitation (i.e. the coastal zones of both slopes). The Ba group with five species is found in the sub-desert shrub communities because of their drought tolerance as well as in the transition zones to the pine forest (only on leeward slopes) due to their moderate cold tolerance.

Group Bb, moderately cold and drought tolerant, is constituted by five species, four of which are regarded as the core species of the 'fayal-brezal': *Erica arborea*, *Myrica faya*, *Ilex canariensis* and *Daphne gnidium*. Group Ab, with three species, is heterogeneous, including representatives of entirely different communities: *Pinus canariensis* (pine forest) and *Petrocephalus lasiospermus* (high mountain shrubland), while the distribution of the third, *Andryalla pinnatifida* overlaps with that of *Pinus*, but extends into the 'fayal-brezal'. *Petrocephalus* probably forms a category of its own, but it is too infrequent in the present material to base a decision on. The single genuine representative of the laurel forest amongst the most frequent species, *Laurus azorica*, has been included in the Bc group (as well as the weed *Origanum virens*). The distribution of *Laurus* overlaps with that of *Erica* and *Myrica* in colder localities.

Group Cb is clearly under-represented on Tenerife; only *Rumex lunaria* is a frequent species in this group. This may be attributed to the absence of well-developed thermophilous forest, as found on other Canary islands, notably El Hierro, La Gomera and Gran Canaria. Species such as *Pistacia atlantica*, *Olea europaea* and *Juniperus phoenicea*, requiring more moisture than the coastal shrubs, but equally high temperatures, are rare on Tenerife.

Five frequent species are indifferent, with a distribution not significantly different from random along the temperature and moisture gradients. Still, three of them are Canarian endemics, including the sixth frequent species *Micromeria varia*. Here, other factors not taken in account in this approach, must be involved, such as human disturbance for *Anagallis*, or local ground water supply for *Rubus*.

Although some climatic guilds are characterized by the principal species of certain vegetation belts, e.g. the sub-desert shrubland and the 'fayal-brezal', there is no general coherence between the guilds and the vegetation belts as described by Ceballos & Ortuño (1951) and Wildpret & del Arco (1987). For instance, species of no less than nine different guilds occur in the pine forest belt dominated by *Pinus canariensis*, guild Ab, e.g. *Pterocephalus lasiospermus* (same guild Ab), *Chamaecytisus proliferus* (Ai), *Asphodelus astivus* (Ba), *Daphne gnidium* (Bb), *Origanum virens* (Bc), *Cistus symphytifolius* (Bi), *Hypericum grandifolium* (Ic), and even *Micromeria varia* (Ii). On the other hand, no thermophilous species (C-groups) do occur here. This broad range of represented guilds reflects the broad range of climatic conditions, especially regarding precipitation, where *Pinus* can dominate the landscape.

As indicated above, environmental factors, not considered in the present climatic approach, will be responsible for the local co-occurrence of species from different climatic guilds, such as local disturbance or ground water availability. Also stochastic dispersal processes may play a part here.

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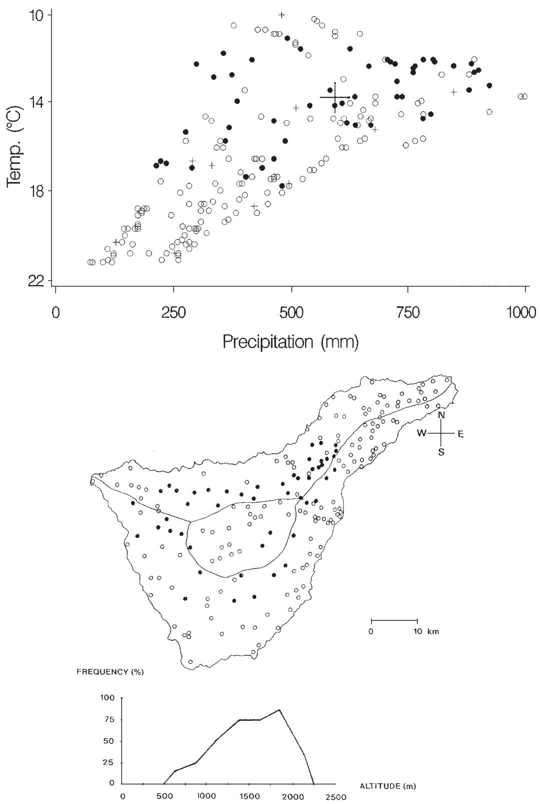
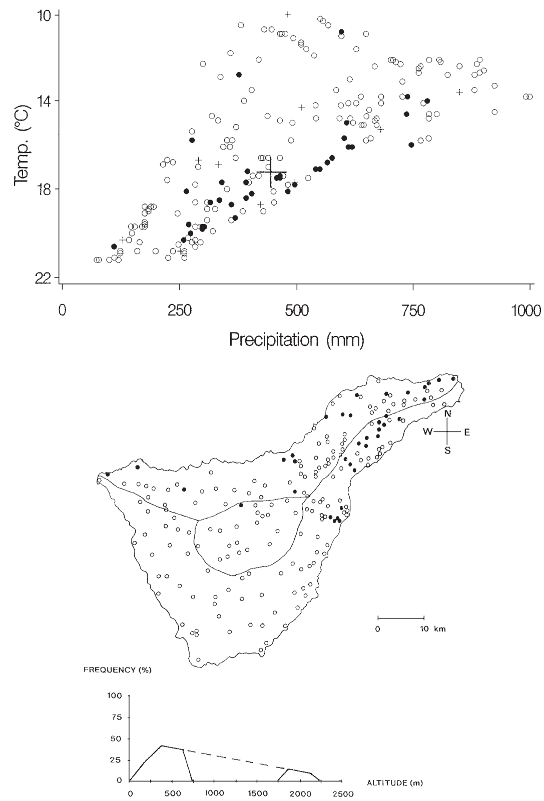
App. 1. Climatic and geographical distribution (black dots) and altitudinal profile (when different for slopes, continuous lines for North and interrupted lines for South slopes) for six species representing different climatic guilds (Table 2). The cross in the figure indicates the centroid of the distribution.

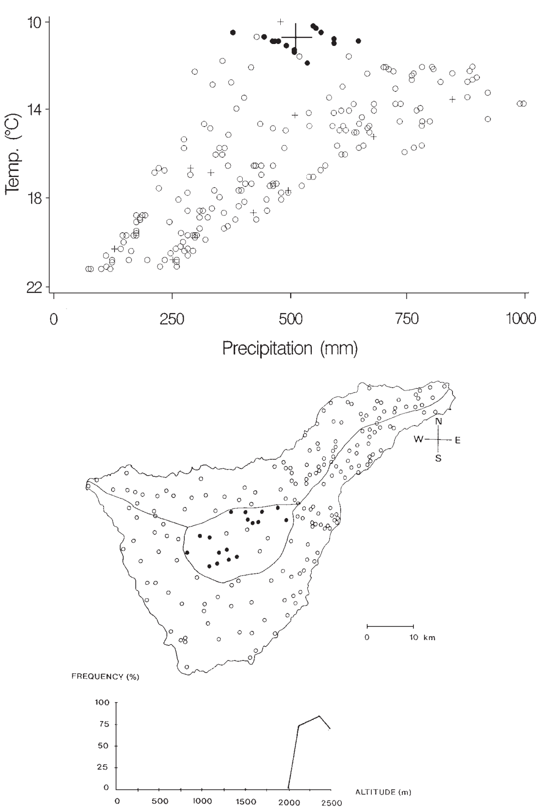
Pinus canariensis



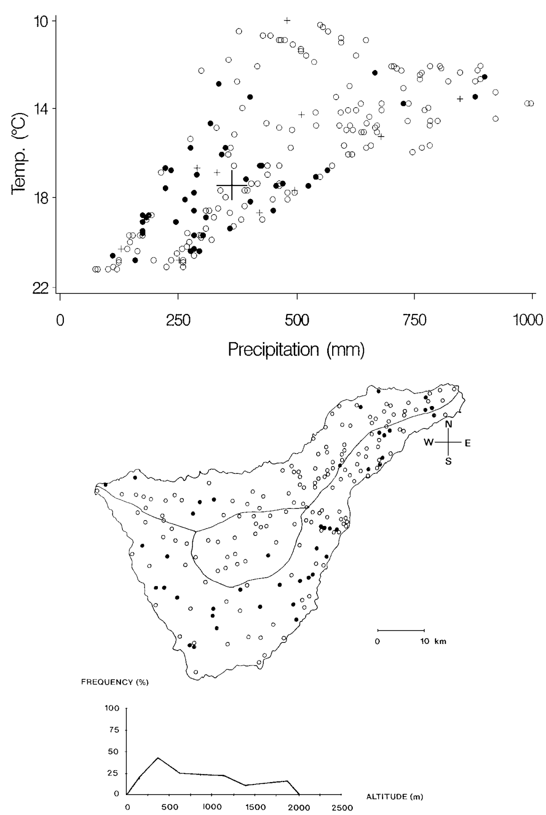
Aspalthium bituminosum

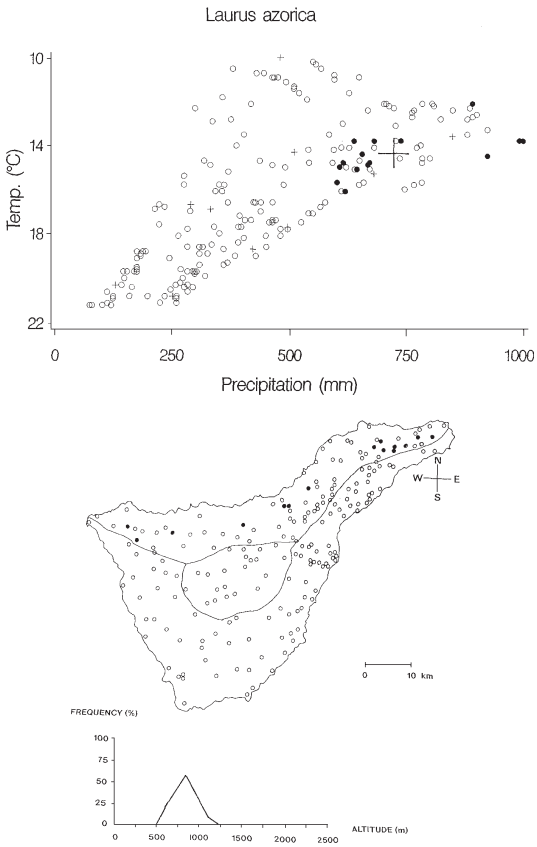


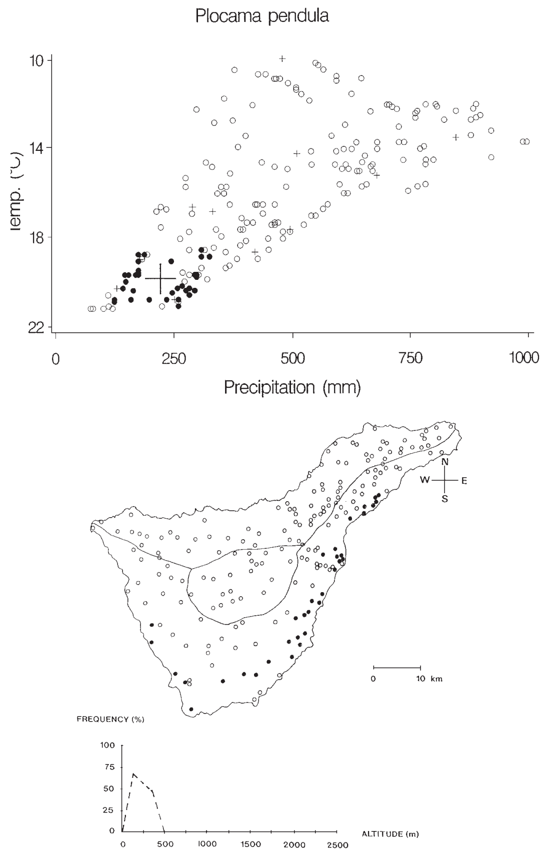
Spartocytisus supranubius



Asphodelus aestivus




Laurus azorica
Temp. (°C)
Precipitation (mm)
N
W
E
S
0 10 km
FREQUENCY (%)
ALTITUDE (m)


Plocama pendula
Temp. (°C)
Precipitation (mm)
N
W
E
S
0 10 km
FREQUENCY (%)
ALTITUDE (m)