

Variation in species composition and vegetation structure of succulent scrub on Tenerife in relation to environmental variation

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Abstract. On Tenerife, the occurrence of environmental gradients over short distances provides a unique opportunity to investigate the relationship between vegetation and environmental factors. In the semi-arid coastal region of Tenerife, floristic composition, species richness and vegetation structure of perennial plants have been studied in 67 locations covering the existing precipitation gradient.

On the island as a whole, variation in species composition could be best explained by mean annual precipitation; at coastal sites, substrate age and soil characteristics also played a significant role. On the other hand, substrate chemistry and the type of eruptive material explained little of the floristic variation. Stand biomass was strongly correlated with mean annual precipitation and was, on the youngest lava flows studied, also affected by substrate age. The native stem succulent species made up the bulk of total biomass along the whole precipitation gradient. Disturbed and undisturbed sites differed significantly in stand biomass and cover. Species richness was correlated with precipitation and substrate age. Distribution of plant functional types was also related to the precipitation gradient. The relative abundance of hemicryptophytes and shrubs with non-hairy leaves increased with increasing precipitation whereas the ratio of shrubs with hairy/non-hairy leaves and succulent plants decreased. Some alien plants were quite frequent at disturbed sites but, on the whole, they contributed little to the species spectrum and to the stand biomass. Undisturbed sites remained almost free of introduced species not considering annuals.

Keywords: Biomass; Canary Islands; Canonical Correspondence Analysis; Plant-available water; Plant functional type; Precipitation gradient; Semi-arid vegetation; Species richness.

Nomenclature: Hansen & Sunding (1993).

Introduction

Climatic factors play an important role in the distribution of plant species and communities at different spatial scales (e.g. Woodward 1987; Kadmon & Danin 1999). In semi-arid regions, the floristic composition and the structure of vegetation were found to be strongly determined by the amount of soil water available to plants (Reid et al. 1990; Skarpe 1990; Cabido et al. 1994; Patten & Ellis 1995), which is, therefore, assumed to be the principal limiting site factor in these regions. Plant-available water is not only related to annual rainfall but also to soil conditions and topography, which modify water-holding capacity, percolation and evaporation rates of the substrate (McDonald et al. 1996; Witkowski & O'Connor 1996; Lane et al. 1998). Large-scale patterns of species distribution are mainly determined by climatic factors whereas other factors like substrate, topography or soil characteristics become more important on smaller spatial scales (Wiens 1989).

In semi-arid conditions, above-ground net primary production and above-ground biomass have also been observed to be related to the availability of soil water (Walter 1984; Lane et al. 1998). This factor limits the carrying capacity of the system. On volcanic islands, primary succession and the age of the substrate can strongly influence species composition and biomass (Aplet et al. 1998). Furthermore, natural and anthropogenic disturbances as dynamic factors frequently alter floristic composition and vegetation structure (Pickett & White 1985; Skarpe 1990). In recent years the plant functional type approach has become a common and useful tool to study vegetation response to climatic changes (e.g. Floret et al. 1990; Díaz & Cabido 1997; Campbell et al. 1999). In semi-arid ecosystems, plant traits linked to hydric stress were found to be closely related to precipitation gradients (Skarpe 1996; Diaz et al. 1998).

Due to the variation of environmental conditions over short distances, Tenerife can be considered an excellent area for studying the relationship between vegetation and environmental factors. Investigations of the functioning of the zonal ecosystems and the species' distribution patterns along ecological gradients have been started only recently (Fernández-Palacios 1992; Fernández-Palacios et al. 1992; Fernández-Palacios & de Nicolás 1995). The response of succulent scrub, the natural vegetation of the coastal regions, to environmental factors has, up-to-now, not been investigated in detail. On Tenerife, well preserved stands of succulent scrub are rare due to human activities. In the past traditional and exportation oriented agriculture, and more recently mass tourism, have, in most places, destroyed the natural vegetation, triggering secondary succession and the establishment of alien species. Heavy grazing pressure of goats during the last centuries has also severely affected the vegetation.

The aim of this paper is to elucidate the relationships between vegetation and environmental factors in order to better understand the functioning of the ecosystem. Multivariate analytical methods were used to identify the ecological factors that best explain the observed floristic and structural variation of succulent scrub. Assuming that plant-available water is the most limiting site factor we tested how closely stand biomass and cover were related to mean annual precipitation and other relevant parameters. Further, we expected that the distribution of different plant functional types would reveal a similar pattern. Finally, as island ecosystems are reported to be easily invaded by alien species (Vitousek et al. 1987; Hughes et al. 1991) we analysed our data also with regard to this aspect.

Study area

On Tenerife, the largest and highest island (2035 km², maximum elevation 3718 m a.s.l.; Fig. 1) in the Canary Archipelago, climate and vegetation vary considerably with altitude and exposure to the prevailing trade-winds (Ceballos & Ortuño 1951; Wildpret & Arco 1987; Marzol 1988) and, therefore, the climatic gradients are particularly steep (Fernández-Palacios & de Nicolás 1995). The climate on Tenerife is greatly influenced by a thermal inversion at around 1200-1500 m a.s.l. that, due to the humid northeast trade-winds, causes the formation of dense clouds on the north-facing slopes of the island (locally known as the 'mar de nubes', sea of clouds), especially during the summer months. The east-west oriented mountain chain divides the island into a humid northern, windward part and a drier southern, leeward part.

At the relatively humid north coast succulent scrub grows up to ca. 300 m a.s.l., at the drier south coast up to 600 m a.s.l. This vegetation type can be found in areas with a mean annual precipitation of 96 to 400 mm (Fig. 2). The arid to semi-arid climate is characterized by a marked dry season from May to September with almost no rainfall and a wet season from October to April. Precipitation is irregular and can be very intensive; in a few days almost a year's rain can fall. In the south, annual fluctuations in precipitation are very pronounced (coefficient of variation = 75%). The number of rainy days and the relative humidity of the air decrease from north to south, while the duration of sunshine, as well as radiation and evaporation increase (Marzol 1988). The mean annual temperature ranges from ca. 17 to 22°C (Fig. 2). At the coast, the amplitude of mean monthly temperature lies around 8°C, i.e. the temperature conditions are rather stable, which is typical of subtropical islands.

Tenerife is of volcanic origin and consists of three old massifs ranging in age from 6.5 to 11.6 million yr (Ancochea et al. 1990). The different eruptive phases on Tenerife have been grouped into four series (Fuster et al. 1968). The few historical eruptions (< 500 yr) reaching coastal areas were not included in this study because they have been severely altered by land use. The soils in the semi-arid coastal regions are usually very poorly developed lithosols, or aridisols with a more or less marked clay-enriched horizon (Fernández-Caldas et al. 1982).

In the coastal regions of Tenerife the natural type of vegetation is succulent scrub (Rivas Martínez et al. 1993), an open shrub vegetation adapted to the subtropical semi-arid climate consisting of stem succulents of the

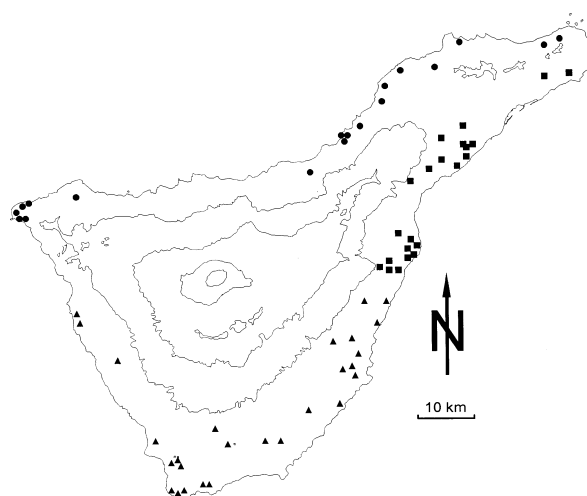


Fig. 1. Location of the 67 study sites on Tenerife separating windward (circles), windward south (squares) and leeward (triangles) sites. The absence of study sites at the northern coast is due to urbanization and the occurrence of banana plantations. Contour lines are indicated at 800 m intervals.

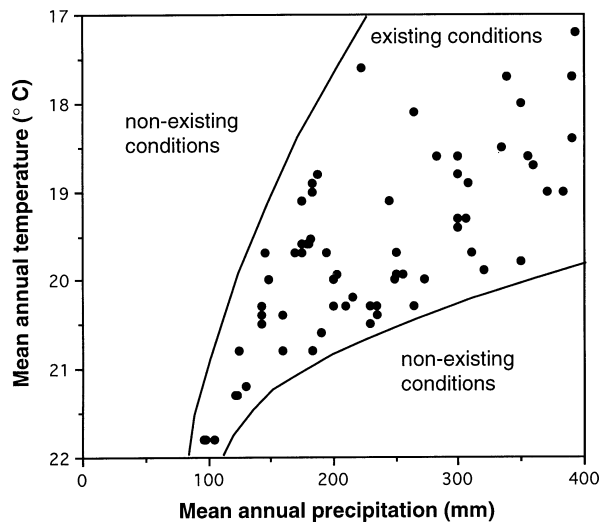


Fig. 2. Existing temperature-precipitation conditions in the area of succulent scrub on Tenerife.

spurge family and leaf succulents or sclerophyllous shrubs that grow up to 4 m high. The landscape is often dominated by the cactus-like *Euphorbia canariensis* (locally known as Cardón) and/or *E. balsamifera* (Tabaiba dulce) and *E. obtusifolia* (Tabaiba amarga). Species composition and phytosociological classification have been studied in detail by Rivas Martínez et al. (1993).

Methods

The basic objective of the sampling design was to cover the whole gradient of water supply conditions in the succulent scrub of Tenerife. More specifically, we followed a stratified sampling strategy based on combinations of several environmental factors, namely (1) altitude: belts of 100 m up to 600 m a.s.l., (2) exposure to wind: windward, windward South and leeward slope, (3) parent rock chemistry: basalt and trachytes/phonolites, (4) parent rock age: four eruptive phases, (5) substrate type: lava flow and pyroclastics, (6) slope: 0-15°, 15-30° and 30-45°, and (7) degree of disturbance of the shrub vegetation distinguishing three groups: (1) little disturbed sites without signs of earlier land uses dominated by climax species; (2) clearly disturbed sites dominated by non-climax species or sites on abandoned fields with non-climax or climax species dominant; (3) sites showing an intermediate degree of disturbance. The third class was not considered when comparing disturbance groups. Communities dominated by annual plants as well as ruderal sites were not included in this study.

Each combination of environmental factors present on Tenerife was represented by a varying number of plots. On the whole, 67 plots of 10 m × 10 m were studied (Fig. 1). A first series of 48 sites were sampled in 1985-1986 (Fernández-Palacios 1992), a second series of 19 sites sampled in 1995-1997 completed the data set (Otto in prep.). At each plot we recorded cover values of all perennial vascular plant species and for those covering > 5%, mainly shrubs, we measured maximum height and maximum diameter of all the individuals. Annual plants were not included in this study because it is very difficult to obtain reasonably complete species lists in this semi-arid environment. The perennial species, especially the shrubs, on the other hand, are slow-growing and species composition does not change much over the years (Cody 2000). More importantly, in contrast to annuals, perennials do not avoid hydric stress and, therefore, are more likely to reflect this environmental factor.

At 12 coastal sites, in addition to the environmental factors mentioned above, the fraction of soil surface covered with rocks was measured with the line-intercept method, using nine 10-m long transects. Five sites on the youngest lava flows were compared with 10 sites on older flows at roughly the same precipitation and temperature range in order to isolate the effect of flow age. Mean annual precipitation and mean annual temperature for all sites were extrapolated from data recorded by the Instituto Nacional de Meteorología at 179 meteorological stations on Tenerife using altitude (Fernández-Palacios 1992). The classification of plant functional types was restricted to a few obvious traits that are related to hydric stress such as life strategy, succulence and hairiness of organs (Werger & Ellenbroek 1978; Orshan 1986).

Above-ground biomass was estimated following the indirect dimensional method (Whittaker & Marks 1975), a non-destructive approach, based on experimentally established allometric regression equations linking biovolume and dry weight of individual plants. We derived such regression curves for the 22 most abundant shrub species of succulent scrub using a power-function model (Fernández-Palacios & de los Santos 1996, Table 1) which follows the equation:

$$B = a Bv^b, \quad (1)$$

where B = Biomass as dry weight, a and b = constants and Bv = biovolume. The apparent plant volume (Bv) was defined by the circular cylinder measured by maximum plant height (h) and maximum diameter (d):

$$Bv = \pi d^2 h / 4 \quad (2)$$

The cylindrical shape of the volume compared with

Table 1. Allometric regression equations and information about origin, life form, water content and biomass accumulation of the 22 most important species to estimate above-ground biomass of succulent scrub on Tenerife (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, n.s. = not significant; ce = Canary endemic; na = native; non-endemic species; me = Macaronesian endemic; i = introduced species; nph = nanophanerophyte; ch = chamaephyte; g = geophyte; suc = stem succulent; n = number of individuals measured).

Species	Origin	Life form	n	r	y-intercept	Slope	Water content (%)	Dry weight (kg/m ³)
<i>Euphorbia canariensis</i>	ce	nph suc	10	0.9723 ***	4.865	0.972	90.1	4.8
<i>Euphorbia balsamifera</i>	na	nph suc	12	0.9969 ***	1.422	1.011	78.8	1.4
<i>Euphorbia obtusifolia</i>	ce	nph suc	11	0.9949 ***	0.764	0.993	73.8	0.8
<i>Plocama pendula</i>	ce	nph	11	0.9445 ***	0.719	1.012	57.8	0.7
<i>Launaea arborescens</i>	na	nph	8	0.9812 ***	1.349	0.941	44.5	1.3
<i>Lycium intricatum</i>	na	nph	6	0.9931 ***	1.191	1.052	34.5	1.2
<i>Kleinia neriifolia</i>	ce	nph suc	6	0.9220 **	0.713	0.736	85.2	0.7
<i>Periploca laevigata</i>	na	nph	5	0.9399 *	0.900	1.245	57.7	0.9
<i>Schizogyne sericea</i>	me	nph	5	0.9969 ***	1.898	1.230	61.7	1.9
<i>Campylanthus salsoloides</i>	ce	nph	5	0.9645 **	0.991	1.064	47.7	1.0
<i>Rumex lunaria</i>	ce	nph	5	0.9213 *	1.866	1.282	61.3	1.9
<i>Neochamaelea pulverulenta</i>	ce	nph	5	0.9841 **	1.139	1.078	43.3	1.1
<i>Rubia fruticosa</i>	me	nph	5	0.9543 *	1.302	1.037	57.1	1.3
<i>Rhamnus crenulata</i>	ce	nph	5	0.9930 ***	0.581	1.099	40.1	0.6
<i>Artemisia thuscula</i>	ce	nph	5	0.9925 ***	0.863	0.907	39.3	0.9
<i>Salsola divaricata</i>	ce	nph	5	0.9842 **	2.824	0.772	35.4	2.8
<i>Lavandula spec.</i>	ce	ch/nph	5	0.9912 ***	0.845	1.027	61.9	0.8
<i>Atalanthus microcarpus</i>	ce	nph	5	0.9687 **	0.199	0.737	64.2	2.0
<i>Ceropegia fusca</i>	ce	ch suc	5	0.9522 *	1.656	0.766	87.2	1.7
<i>Opuntia spec.</i>	i	nph suc	4	0.9998 ***	2.831	0.999	90.8	2.8
<i>Urginea hesperia</i>	ce	g	4	0.9694 *	0.076	0.590	88.1	0.1
<i>Asphodelus aestivus</i>	na	g	4	0.9484 *	0.732	1.134	83.5	0.7

other types of volume, like elliptical cylinder or paraboloid of rotation, has been found to provide a simple and sufficiently accurate estimate of the aerial biomass of shrubs (Usó et al. 1997). Among the tested possible equations, power-functions showed the highest correlation coefficients for all species. For the three very abundant *Euphorbia* species at least 10 individuals were analyzed to ensure high correlation coefficients. Aplet et al. (1998) also worked with the power-function model for biomass estimation whereas Usó et al. (1997) found the exponential model more adequate. After the destructive process of establishing species-specific regression curves we were able to estimate in a non-destructive way above-ground biomass of all 67 stands, based on heights and diameters of the individuals present. For some of the rare species that reached more than 5 % cover we did not establish specific regression curves but used the equations of species with similar growth forms. Species composition was analysed using Detrended Correspondence Analysis (DCA; Hill 1979). In order to investigate the nature of the relationship between vegetation variation and environmental factors we selected Canonical Correspondence Analysis (CCA, ter Braak 1986). In CCA, ordination axes are constrained linear combinations of the environmental variables included. If there are no fundamental differences between the results of DCA and CCA, probably all important

environmental variables have been taken into account. For the ordinations cover abundance values were log-transformed and rare species were downweighted. The significances of the eigenvalues of the ordination axes were tested using the Monte Carlo test with 5000 iterations. The importance of each environmental variable was evaluated by forward stepwise regression using the Monte Carlo permutation test with the same number of iterations.

Linear regressions between biomass and species richness, on the one hand, and all the quantitative environmental variables, on the other hand, were calculated using log-transformed values for biomass. For ordinal variables the Kruskal Wallis test was applied. Differences between disturbed and undisturbed sites were analyzed by comparing the slopes and elevations of the corresponding linear regression equations. Significant differences between sites on the youngest lava flows and sites on older flows were evaluated by the U-Mann Whitney test. In order to obtain robust correlation values and to reduce the probability of a type I error, we applied a correction for non-independent multiple comparisons (Holm 1979). We followed the statistical procedures of Zar (1984) using the SPSS statistical package (Anon. 1990) and the CANOCO package (ter Braak & Šmilauer 1998).

Results

Species composition

In the 67 samples, 124 species of perennial vascular plants were found, comprising seven geophytes, 10 graminoids, nine hemicryptophytes, 36 chamaephytes and 62 nanophanerophytes. 15.3 % of the species are endemic to Tenerife, 46.8 % endemic to the Canary Islands and 4.0% endemic to Macaronesia (the Atlantic islands including Azores, Madeira, Selvagens Islands and Cape Verde). 23.4% are not endemic, but native to the Canarian flora, and 10.5 % must be classified as introduced. In total, 66.1 % of the species sampled are endemic. The 13 alien species include three geophytes, three graminoids, one hemicryptophyte and six shrubs. Aliens occurred on 33 of the 67 sites sampled, but they were more common on disturbed sites (80% frequency) than at undisturbed sites (33.3%). Likewise, the mean percentage of introduced species per plot is significantly higher on disturbed as compared to undisturbed sites (3.1 % vs. 8.0 %, $p < 0.01$). Only four alien species reached a cover of more than 5 % (*Opuntia ficus-barbarica*, *O. dillenii*, *Agave americana* and *Spartium junceum*). Only the two *Opuntia* species were present in more than 5 % of the plots studied.

If all sites are considered, an average number of 11.9 species per 100 m² (range: 5 to 25) was recorded. At undisturbed sites, species richness was found to correlate positively with precipitation but seemed to be also influenced by substrate age (Table 2). At coastal sites on basaltic lava flows, species richness was negatively correlated with the percentage of rocks at soil surface, whereas precipitation accounted for little of the variance. On the youngest lava flows and at disturbed sites, species numbers were significantly lower than on older flows and undisturbed sites (9.6 vs. 11.3, and 11.4 vs. 12.6, respectively, species/100 m², $p < 0.05$).

In a first step a DCA ordination of all 67 samples was performed to find floristic gradients. The eigenvalues of the first three axes were 0.480, 0.277 and 0.185,

respectively; the first axis had a gradient length of 3.897 SD, almost equal to a full turnover in species composition that occurs in about 4 SD (Gauch 1982). In a second step we applied CCA ordinations including the environmental variables. The first CCA axis of the ordination of the 67 samples (eigenvalue analysis = 0.366, $p < 0.001$) showed strong correlations with precipitation and temperature (Fig. 3a). Mean annual temperature and mean annual precipitation were negatively correlated with each other. Altitude was also correlated with precipitation partly for methodological reasons (extrapolations). All other environmental variables seemed to explain little of the floristic variation. On the whole, the first CCA axis corresponded to an aridity gradient, separating dry and warm sites from wetter and cooler ones. The second axis (eigenvalue analysis = 0.141, $p < 0.01$) represented a wind exposure gradient. In the ordination diagram (Fig. 3a) the two groups of leeward and windward sites could clearly be distinguished. Furthermore, the second axis was related to the volcanic material since phonolitic/trachitic pyroclastics are more frequent in the south, although the influence was not very strong. Stepwise regression with the Monte Carlo permutation test showed that slope, substrate age, substrate type and chemistry showed little relations to species composition.

When disturbed and undisturbed sites were analysed separately, precipitation and temperature were still the most important environmental variables correlated with the first canonical axis, whereas wind exposure was related to the second axis. At undisturbed sites, precipitation showed clearly the strongest correlation with the first CCA axis (eigenvalue analysis = 0.347, $p < 0.01$) and, therefore, explained best the floristic variation, which was represented in the biplot by the 50 most important species (Fig. 3b).

At coastal sites on basaltic lava, where some soil characteristics are available, the first axis (eigenvalue analysis = 0.406, $p < 0.05$) was again strongly correlated with precipitation while the second axis (eigenvalue analysis = 0.241) represented a gradient of substrate rockiness that is related to soil type and substrate age (Fig. 3c).

Table 2. Significant correlations of environmental variables with stand biomass and species richness. The effect of the ordinal variable substrate age was evaluated using the Kruskal-Wallis test (K-W) instead of a linear regression. At coastal sites this test could not be applied due to the low number of plots. p -values were corrected for multiple comparison (* = $p < 0.05$, *** = $p < 0.001$).

Dependent variable	Independent variable	Undisturbed sites		Disturbed sites		Undisturbed coastal sites	
		r^2	p	r^2	p	r^2	p
Log biomass	Precipitation	0.764	0.0004 ***	0.431	0.0004 ***	0.920	0.0004 ***
Log biomass	Temperature	0.325	0.0133 *	0.319	0.0152 *	0.335	0.0531 n.s.
Log biomass	Substrate age	K-W	0.0487 *	K-W	0.0519 n.s.	-	-
Species richness	Precipitation	0.245	0.0348 *	0.0016	0.8329 n.s.	0.129	0.2520 n.s.
Species richness	Substrate age	0.190	0.0460 *	K-W	0.1225 n.s.	-	-
Species richness	Rockiness	-	-	-	-	0.578	0.0246 *

Biomass and cover

The 22 most abundant species, mainly endemic or native, non-endemic shrubs, that were used to estimate above-ground biomass of succulent scrub on Tenerife, are represented in Table 1. We could distinguish three species groups: (1) species with high water contents (>70%) with all stem succulents and geophytes, (2) species with intermediate water contents (50–70 %) and (3) species with low water contents (< 50%). The native cactus-like stem succulent *Euphorbia canariensis* showed the highest water content (> 90%) and the highest weight per volume, i.e. the highest biomass accumulation. The lowest water content, 34.5 %, was measured for *Lycium intricatum*, a mediterranean thorn shrub.

Total above-ground biomass of the succulent scrub stands studied varied substantially across the island (range: 0.09 to 5.25 kg/m²). Two major factors explain this variability. First, community biomass increased exponentially with precipitation on disturbed and undisturbed sites (Table 2, Fig. 4a,b). Second, disturbance itself had a dramatic effect on biomass since the differences between the two regression curves were highly significant ($p < 0.01$). Therefore, the highest biomass levels we found at the wind exposed north coast, at undisturbed sites at high elevations with high precipitation, the lowest biomass at the south coast, on disturbed sites at low elevations with low precipitation.

Mean annual temperature was negatively correlated with biomass but the correlation was not as strong as the positive correlation with precipitation (Table 2). At undisturbed sites, biomass seemed to be also related to substrate age. A comparison of sites on young and older lava flows with roughly the same precipitation and temperature regimes revealed that the biomass of succulent scrub growing on the youngest lava flows was significantly lower (0.9 vs. 1.2 kg/m², $p < 0.01$). Stepwise regression of biomass on the four environmental variables showed that on all the sites (all the disturbed sites, all the undisturbed sites and all the undisturbed coastal sites) mean annual precipitation was the most important factor.

The percentage of biomass contributed by native stem succulents (eight species) was, as expected, quite high at undisturbed sites (74.1%, range: 23% to 94%), but surprisingly it did not vary with precipitation. Introduced stem succulents (two *Opuntia* species) contributed only very little to the total biomass (2.3%). On disturbed sites, in contrast, native stem succulents showed significantly lower, introduced stem succulents higher values (74.1 % vs. 37.8 %, and 2.3 % vs. 14.6 % of the total biomass respectively; $p < 0.01$). In contrast to biomass, vegetation cover showed a linear relationship with precipitation (Fig. 4c, d). The differences between undisturbed and disturbed sites were also significant

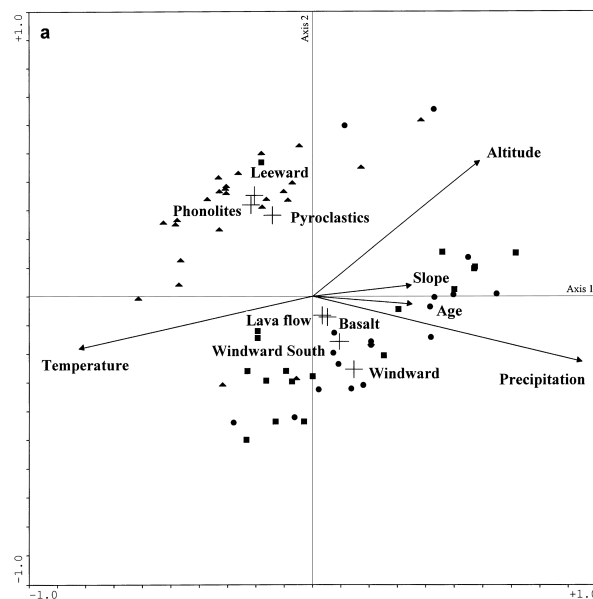
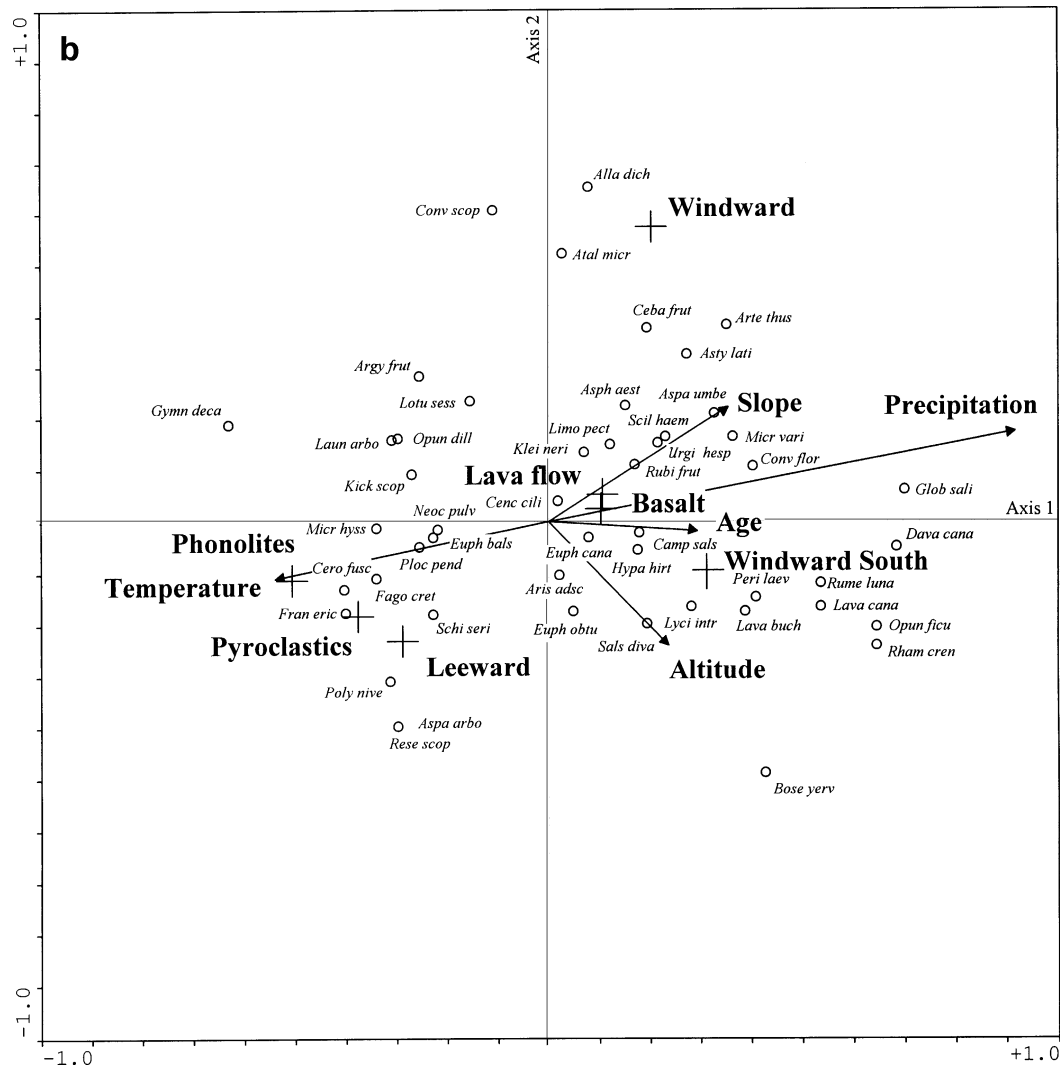


Fig. 3. CCA ordinations showing biplots for the ordination axes 1 and 2 of: **a.** Sites and environmental variables for all 67 sites (circles for windward, squares for windward South and triangles for leeward sites), **b. (overleaf)** species and environmental variables for 27 undisturbed sites displaying scores of the 50 most important species and **c. (overleaf)** sites and environmental variables for 12 undisturbed coastal sites on basaltic lava. Centroids of the binary variables are represented with a cross, continuous variables with an arrow.

Species abbreviations include:

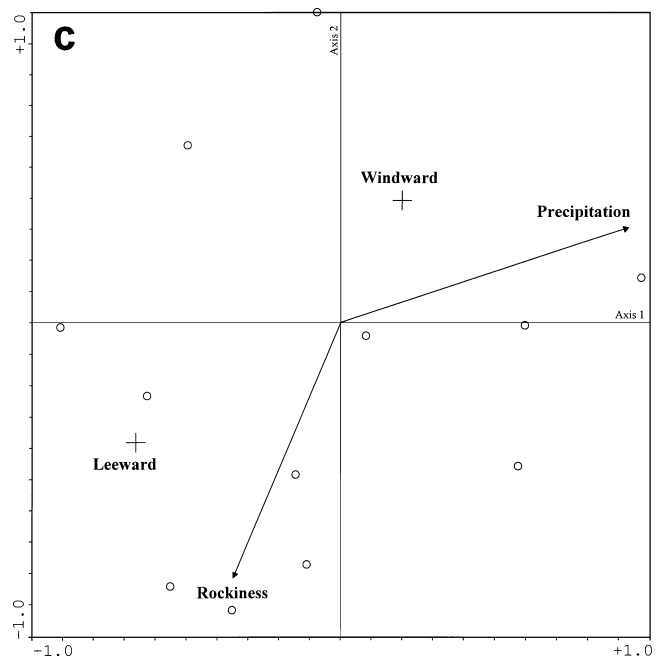
Allagopappus dichotomus (Alla dich), *Argyranthemum frutescens* (Argy frut), *Aristida adscensionis* (Aris adsc), *Artemisia thuscula* (Arte thus), *Asparagus arborescens* (Aspa arbo), *Asparagus umbellatus* (Aspa umbe), *Asphodelus aestivus* (Asph aest), *Astydemia latifolia* (Asty lati), *Atalanthus microcarpus* (Atal micr), *Bosea yervamora* (Bose yerv), *Campylanthus salsoloides* (Camp sals), *Ceballosia fruticosa* (Ceba frut), *Cenchrus ciliaris* (Cenc cili), *Ceropegia fusca* (Cero fusc), *Convolvulus floridus* (Conv flor), *Convolvulus scoparius* (Conv scop), *Davallia canariensis* (Dava cana), *Urginea hesperia* (Urgi hesp), *Euphorbia balsamifera* (Euph bals), *Euphorbia canariensis* (Euph cana), *Euphorbia obtusifolia* (Euph obtu), *Fagonia cretica* (Fago cret), *Frankenia ericifolia* (Fran eric), *Globularia salicina* (Glob sali), *Gymnocarpus decander* (Gymn deca), *Hyparrhenia hirta* (Hypa hirt), *Kickxia scoparia* (Kick scop), *Kleinia neriifolia* (Klei neri), *Launaea arborescens* (Laun arbo), *Lavandula buchii* (Lava buch), *Lavandula canariensis* (Lava cana), *Limonium pectinatum* (Limo pect), *Lotus sessilifolius* (Lotu sess), *Lycium intricatum* (Lyci intr), *Micromeria hyssopifolia* (Micr hyss), *Micromeria varia* (Micr vari), *Neochamaelea pulverulenta* (Neoc pulv), *Opuntia ficus-barbarica* (Opun ficu), *Opuntia dillenii* (Opun dill), *Periploca laevigata* (Peri laev), *Plocama pendula* (Ploc pend), *Polycarpha nivea* (Poly nive), *Reseda scoparia* (Rese scop), *Rhamnus crenulata* (Rham cren), *Rubia fruticosa* (Rubi frut), *Rumex lunaria* (Rume luna), *Salsola divaricata* (Sals diva), *Schizogyne sericea* (Schi seri), *Scilla haemorrhoidalis* (Scil haem).

($p < 0.01$). On the youngest lava flows, vegetation cover was significantly lower than on the older flows (40.8 % vs. 66.2 % cover, $p < 0.01$). Comparing the regression curves stand biomass and cover of disturbed sites reached an average of 21.6 % and 62.6 % of the levels of mature stands, respectively.



Species origin and functional types

At undisturbed sites, the relative number of endemic (Canarian and Macaronesian) species correlated positively with mean annual precipitation, whereas the relative number of native, non-endemic species correlated negatively. The number of introduced species was not correlated with precipitation (Table 3). The relative number of hemicryptophytes and shrubs with non-hairy leaves increased significantly with precipitation. On the other hand, chamaephytes and shrubs with succulent stems or leaves as well as the ratio of shrubs with hairy/non-hairy leaves correlated negatively with precipitation (Table 3). Geophytes were more abundant on wet sites, stem succulents and shrubs with hairy leaves on dry sites, but correlations were not significant (after



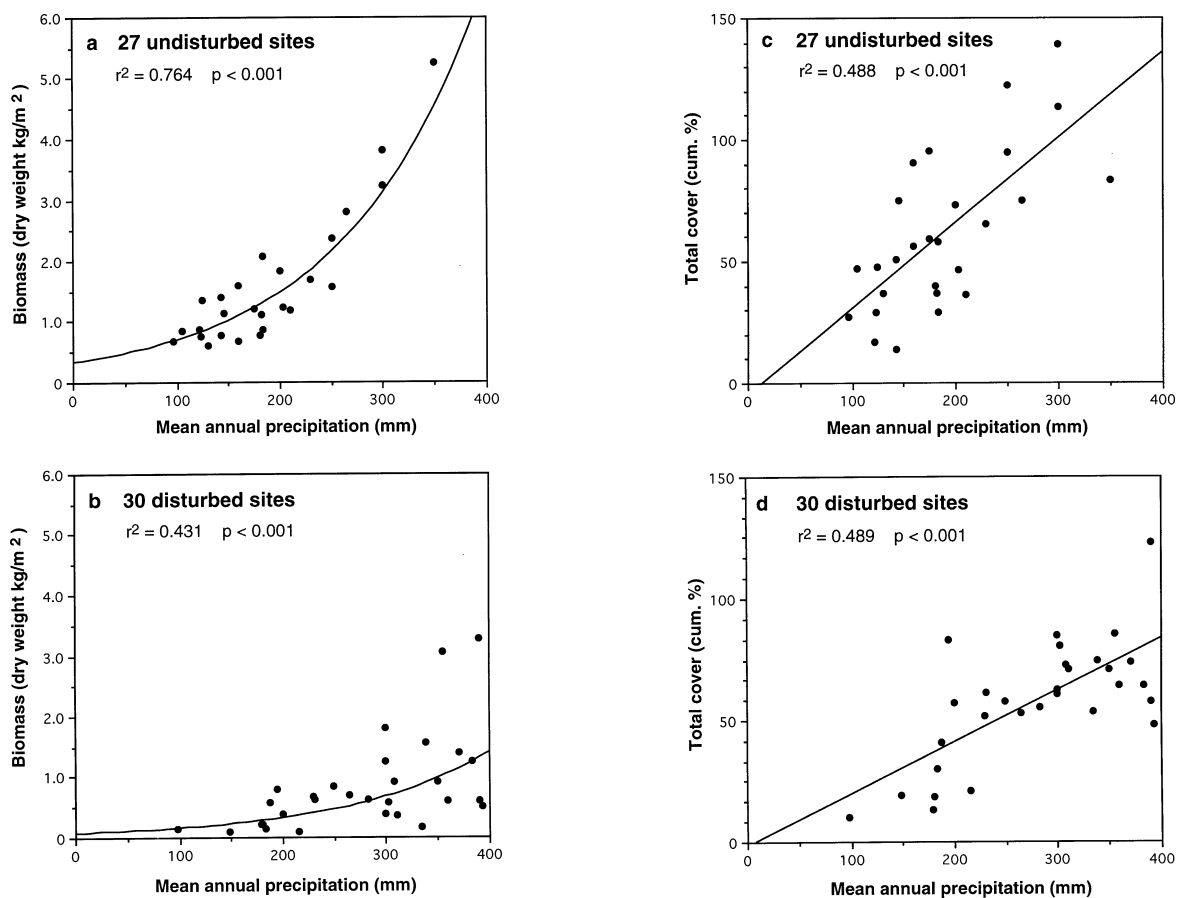


Fig. 4. Regressions between precipitation and structural data, (a) biomass at undisturbed sites, (b) biomass at disturbed sites, (c) total cover at undisturbed sites and (d) total cover at disturbed sites.

correction for multiple comparison). Perennial graminoids were regularly distributed along the precipitation gradient. On disturbed sites, by contrast, functional types did not correspond to the precipitation gradient.

Discussion

Climate

Although we cannot clearly separate the influence of precipitation, temperature and altitude due to covariation, mean annual precipitation seems to be the environmental factor that explains best the variation in species composition, species richness, structure and the distribution of plant functional types of the succulent scrub on Tenerife. Fernández-Palacios (1992) and Fernández-Palacios & de Nicolás (1995) showed that hydric and thermic stress have a great influence on the species distribution and the altitudinal vegetation pattern on

Table 3. Correlations of precipitation with the relative abundance of different species groups at undisturbed sites. p -values were corrected for multiple comparison (* = $p < 0.05$).

Species group	r	p
Canary endemics	0.513	0.0310 *
Native, non-endemic species	-0.582	0.0112 *
Introduced species	0.216	0.2782
Geophytes	0.402	0.0909
Perennial graminoids	0.004	0.9826
Hemicryptophytes	0.564	0.0154 *
Chamaephytes	-0.462	0.0310 *
Phanerophytes	0.075	0.7091
Shrubs with succulent leaves	-0.028	0.6859
Shrubs with succulent stems	-0.414	0.0872
Stem and leaf succulents	-0.437	0.0478 *
Shrubs with hairy leaves	-0.431	0.0684
Shrubs with non-hairy leaves	0.439	0.0438 *
Ratio hairy/non-hairy leaves	-0.525	0.0239 *

Tenerife. Compared to the 20 °C differences in mean annual temperature observed on the whole island, the 5 °C temperature range in the succulent scrub is relatively small. Moreover, in the study area the temperature range is close to the optimum for plant growth, i.e. 15 - 25 °C (Larcher 1995). In addition, the succulent scrub is not subject to frost events (Höllermaun 1980) and does not reach the altitude of the sea of clouds, which, on the north coast, starts ca. 600 m a.s.l., and can, therefore, not profit from the horizontal fog drip. Consequently, it is assumed that in the area studied mean annual temperature is much less important than annual precipitation. This is supported by the result of the CCA ordination of the undisturbed sites.

However, due to the sea of clouds, in the coastal region in the north of the island air humidity and the number of cloudy and rainy days are higher, evaporation and temperature amplitudes smaller than in the south. This climatic effect is represented by the factor wind exposure which seemed to explain some of the floristic variations since it was always related to the second ordination axis.

In contrast to temperature, soil water availability has a strong influence on net primary productivity in arid or semi-arid ecosystems (Lane et al. 1998). A linear relationship between mean annual precipitation up to 500 mm and above-ground dry weight of grass and shrub vegetation has been reported by Walter (1984). We found an exponential correlation between biomass and precipitation but a linear correlation between vegetation cover and precipitation. Possibly, the relationship biomass/precipitation is linear in open shrub- and grassland, but becomes exponential when vegetation height increases considerably, i.e. when the third spatial dimension becomes important.

The increase of the relative number of native, non-endemic species with decreasing precipitation at undisturbed sites can be explained by the relationship of succulent scrub with shrub communities in northern Africa (Bramwell 1976; Santos 1983). Many of the species, which are especially abundant in the dry southern parts of the island, grow also on the western coast of Africa, i.e. *Euphorbia balsamifera*, *Launaea arborescens*, *Fagonia cretica*, *Lotus glinoides*, *Frankenia ericifolia* and *Eremopogon foveolatus*. In the northern parts with better water availability Canarian endemics dominate the species spectrum.

The correlation of species richness with precipitation can be interpreted as a relationship of productivity or energy flow rate and diversity (Rosenzweig & Abramsky 1993). In this context, succulent scrub would be placed in the increasing-phase of the unimodal productivity-diversity-function since we could not observe a decline of species richness at sites with high water supply.

Plant functional types have become a common and useful tool to study vegetation response to climatic changes (Floret et al. 1990; Skarpe 1996; Díaz & Cabido 1997; Campbell et al. 1999). Our results show that the occurrence of succulence (of stems and leaves) and leaf hairiness are related to water stress. Although stem succulents (primarily the five *Euphorbia* species) were more dominant in the species spectrum on dry sites, their contribution to the total biomass was not influenced by the precipitation gradient. Stem succulence (with or without deciduous leaves) seems to be the most successful life strategy over the whole range of water supply conditions in the semi-arid regions of Tenerife. Therefore, the term 'succulent scrub' is reasonable, even though out of 124 perennial plant species only eight are stem succulents. With increasing rainfall species richness and the number of shrubs that are less adapted to hydric stress increase while stem succulents still dominate. If water-supply conditions are suitable for tree growth, stem succulents will be probably outcompeted by small trees of the thermophilous forest, which, on Tenerife, replaces the succulent scrub at higher altitudes.

Other life strategies such as geophytes, hemicryptophytes and chamaephytes were also found to correlate with the precipitation gradient. Similar results are reported from Israel by Danin & Orshan (1990). On a precipitation gradient from 50 to 400 mm chamaephytes decreased significantly while both hemicryptophytes and geophytes increased. Chamaephytes are better adapted to summer drought than phanerophytes since their transpiring and assimilating surfaces are smaller. Therophytes are expected to be better adapted to drought than geophytes and hemicryptophytes.

Substrate age and type

Aplet et al. (1998) who studied Hawaiian lava flows found that, apart from precipitation and temperature, lava flow age strongly influenced species composition and biomass. Substrate age seemed to influence species composition, species richness, stand biomass and cover only on young lava flows (< 10 000 yr) in the semi-arid coastal region of Tenerife. Soil development is very slow during primary succession because parent rock alteration and accumulation of organic matter is limited by soil moisture. In addition to the low water storage capacity of the soils, the availability of nitrogen could also be a limiting factor for biomass on basaltic lava flows at least for the first 1000 yr as observed in Hawaii (Vitousek & Walker 1987). Soil and vegetation development are affected not only by parent rock age and climatic factors but also by the lava flow texture (González-Mancebo et al. 1996; Aplet et al. 1998),

which was not taken into account in this study. However, rockiness that was correlated with the second ordination axis and species richness at undisturbed coastal sites is related to both substrate age and lava flow texture. In arid climates, rockiness of the substrate, soil texture, soil depth and topography can affect the amount of plant-available soil water (Reid et al. 1990; Parker 1991; McDonald et al. 1996; Witkowski & O'Connor 1996; Lane et al. 1998).

In agreement with the findings of Fernández-Palacios & de Nicolás (1995), the chemical composition (phonolitic/basaltic) and the type of eruptive material (lava flow/pyroclastics) did not seem to explain much of the variation in species composition of the succulent scrub. The salic pyroclastics frequent in the southern parts of the island were closely related to the factor wind exposure. Local studies should be carried out to separate clearly the influence of the two factors.

Disturbance and alien species

Disturbance had a strong effect on stand biomass and cover. Plant individuals are usually younger and smaller at successional stages, as vegetation has not yet reached the carrying capacity of the system, determined primarily by the water availability. In spite of the heterogeneity of the disturbed sites regarding type, intensity and duration of disturbance, our results indicate that changes in vegetation structure of succulent scrub during secondary succession are also influenced by the dominant precipitation gradient. At disturbed sites, stand cover regenerates faster than stand biomass because the open space is filled out by individuals first in the horizontal and then in the vertical dimension. Advanced stages of retrogressive or progressive secondary succession of succulent scrub are generally formed by endemic and native, non-endemic species, typical elements of this scrub type that often have a wide ecological amplitude and a certain ruderal character (Fernández-Palacios 1992). The observations that species richness was also affected by disturbance and that, at disturbed sites, functional types were not correlated with precipitation, can probably be explained by the lower level of competition and community organisation during succession.

The fact that annuals and heavily disturbed sites – such as ruderal places or early successional stages on abandoned fields – were not included in this study, can explain the low percentage of alien plants found. Although some aliens were quite frequent, especially on disturbed sites, their relative importance regarding species spectrum, vegetation cover and stand biomass was low. Kunkel (1976) presented a list of 35 aggressive elements of alien flora on the Canary Islands, which could endanger natural ecosystems. The two introduced

Opuntia species can, in fact, dominate on disturbed sites; *Opuntia dillenii* more on the dry southern part of Tenerife and *O. ficus-barbarica* in more humid northern regions. This is probably mostly the result of both the centuries-long degradation caused by grazing goats and due to the cultivation of the latter species for producing Cochenille during the last centuries for exportation. The *Opuntia* species are succulents and have the same life strategy as the native *Euphorbia* species but with the advantages of protective spines and highly effective vegetative reproduction. Nevertheless, it is doubtful whether they can actively encroach and eventually dominate mature stands of succulent scrub but surely they can influence the succession processes. The African perennial grass *Pennisetum setaceum*, an invasive plant and a problem on the Canary Islands as well as on Hawaii (Hughes et al. 1991; García-Gallo et al. 1999), occurred only on two of the sampled plots and with very low abundance. Although this plant has invaded huge areas in the semi-arid zone of the Canary Islands it has not yet reached undisturbed sites of succulent scrub on Tenerife. This supports the idea that the susceptibility of island ecosystems to invasive plant species is, among other factors, related to the degree of disturbance (Aplet et al. 1998).

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