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Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands)

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Abstract

Roadside plant communities were studied along two roads following an altitudinal gradient in Gran Canaria and Tenerife (Canary Islands). Our aim was to investigate variation in plant species richness, particularly of the alien flora, along a gradient from coastal shrubland to summit vegetation (1950 m a.s.l. in Gran Canaria, 2300 m in Tenerife) in relation to variation in habitat factors (altitude, habitat structure, roadside disturbance, distance to urban nuclei). We compared different species groups that were classified in terms of their biogeographical status, origin and life form. Altitude was the most important factor determining species richness and composition along both roadside transects. Alien plants showed a unimodal distribution pattern along the altitudinal gradient, with less species and lower abundance at low and high altitudes, and highest abundance at intermediate altitude. Alien plant species were also relatively more frequent near urban centres. The number of native and alien species was significantly positively correlated along the altitudinal gradient. Both alien and native, non-endemic species showed differences in their distribution along the altitudinal gradient according to their biogeographical affinities and climatic tolerances. Despite considerable differences in species pools these patterns were consistent among the two islands. Environmental (abiotic) stress is proposed as a primary, altitude-related factor acting as a filter against most alien plants at coastal and highmountain altitudes. A higher frequency or intensity of disturbance at intermediate altitudes may be a further causal factor promoting alien plants in this zone. Future management efforts to control alien plants along roads should, therefore, concentrate on intermediate altitudinal zones of the higher Canary Islands.

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Keywords: Alien species; Altitudinal gradient; Disturbance; Invasive plants; pDCCA; Quadratic regression

Introduction

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The composition of an alien flora, and the frequency and invasiveness of alien plants in introduced areas can be influenced by climate, geology, land use, landscape context, competition with natives, and natural or

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anthropogenic disturbance (Crawley, 1987; Wilson et al., 1988, 1992; Alpert et al., 2000; Richardson et al., 2000; Pyšek et al., 2002; Rejmánek et al., 2005). Therefore, identifying the factors that influence the distribution of alien species across a landscape is fundamental for evaluating the present and future extent of plant invasions and for development of eradication programs (Wace, 1977; Alpert et al., 2000; Rejmánek and Pitcairn, 2002). In addition, the similarity in climatic conditions between the native area of a species and its introduced area may be an important factor delimiting the potential range of an invasion. Investigating the relationship between climatic matching and invasion success is also important for evaluating how invasive species might spread under climate change.

Mountain systems are highly suitable for investigating such relationships, particularly the relative importance of climatic limitation, community invasibility and propagule pressure (Becker et al., 2005; Daehler, 2005; McDougall et al., 2005). Steep climatic gradients in mountain systems may also provide a convenient study system to draw inferences for potential range extensions of invasive plants across latitudes (Stohlgren et al., 2005).

Besides endemic and native plant species the Canary Islands harbour introduced and invasive plants of (sub-) tropical, mediterranean and temperate origin (Izquierdo et al., 2001). Strong variation in altitude and aspect, which define local mesoclimatic zones, and land use, are primary factors in structuring both native and alien plant communities on the higher Canary Islands (Fernández-Palacios and de Nicolás, 1995; Whittaker, 1998; Silva and Smith, 2004).

In this study we investigate plant species distributions on two Canary Islands along roadside gradients. Despite the importance of roads as corridors and habitats for alien species (Trombulak and Frissell, 2000; Forman et al., 2002), roadside vegetation of oceanic islands is not well studied. On continents, native ruderal and alien species predominate along roads, and the species richness of these groups is commonly higher along road edges than within natural habitats (Ullmann and Heindl, 1989; Benninger-Truax et al., 1992; Ullmann et al., 1995). Once established at roadsides, alien species may spread along these corridors due to traffic, wind, water or animals, contributing to homogenize the roadside communities (Clifford, 1959; Greenberg et al., 1997). Roads may also represent a 'latent' reservoir of propagules of alien plants which might eventually surpass a threshold and colonize adjacent natural areas where (or when) their ecological requirements are met (Milberg and Lamont, 1995).

The role of roadsides as corridors and habitats for the abundance and composition of alien vs. native plant assemblages has been rarely assessed along altitudinal gradients (Pauchard and Alaback, 2004), especially on islands (Ullmann et al., 1995). On oceanic islands with strong altitudinal climatic gradients over relatively short distances roadsides, as highly disturbed and relatively uniform habitats with few barriers to dispersal, provide herbaceous alien species with the opportunity to reach the distribution limits with respect to their biogeographical affinities and environmental tolerances (Wilson et al., 1992). Therefore, roadsides on oceanic islands represent excellent structures for investigating the responses of alien species to environmental variation (Ullmann et al., 1995).

By studying the plant communities along two roads spanning the full elevation gradient from coastal areas to the (sub-)alpine summits in two Canary Islands, we aimed to investigate how the distribution of alien plant species relates to altitude, disturbance and potential source populations compared with native plant species. We also analysed whether species groups with distinct biogeographical and climatic origin differed in their distribution along these environmental gradients. The current study represents the first record of roadside vegetation from the Canary Islands.

Material and methods

Study areas

The study was conducted on Gran Canaria and Tenerife, two central volcanic islands of the Canary Islands group, which is situated in the subtropics ca. 70 km off the NW-coast of Africa $(27-29^{\circ}N, 13-18^{\circ}W)$; Fig. 1). Tenerife is the largest and highest island of the Canarian archipelago and of whole Macaronesia. It encompasses an area of 2033 km² and reaches 3718 m a.s.l. at the peak of the Teide. Gran Canaria is slightly smaller (1560 km²) and does only reach up to sub-alpine altitudes (highest peak at 1949 m). On these mountainous islands the prevailing trade winds create a contrast between humid NE (windward) slopes and the more arid SE-SW (leeward) slopes (Fernández-Palacios, 1992). The main climatic feature is an orographic cloud layer caused by an inversion in temperature and humidity on the windward slopes at c. 1200 m a.s.l. (Fernández-Palacios, 1992).

The natural vegetation is structured altitudinally from coast to summit in several vegetation belts, namely coastal scrub, thermophilous woodland, laurel forest (mainly at the windward slope), *Pinus canariensis* forest and summit scrub. Vegetation types are not strictly discontinuous along the elevation gradient (Fernández-Palacios and de Nicolás, 1995). On Tenerife, discontinuity in the vegetation is more sharply defined on the windward slope than on the leeward slope (Fernández-Palacios, 1992), where vegetation mostly resembles a



Fig. 1. Tenerife and Gran Canaria islands, with the road segments studied shown as bold lines (altitudinal contours indicate 500, 1000, 1500, 2000 and 2350 m a.s.l.).

coenocline or vegetation continuum (Whittaker, 1975). Gran Canaria shows similar vegetation belts excluding the summit scrub. Both, Gran Canaria and Tenerife are heavily populated (ca. 900.000 and 700.000 inhabitants, respectively). Because the large villages are located mainly near the coast, human pressure decreases with altitude, with low human population above 1000 m altitude.

We surveyed second-class paved roads that do not have a shoulder (Pérez, 2000). The selected roads on both islands were two-lane corridors with an average width of 7 m. Traffic density was similar for both study roads (between 1000 and 5000 cars day⁻¹). One road transect was established on each island from the sea level to the highest altitude possible (pine forest in Gran Canaria, summit scrub in Tenerife). These roads were chosen to encompass the whole altitudinal gradient.

The road transect on Gran Canaria ran from the sea level to 1950 m a.s.l. on the east slope, which is partially affected by trade winds (Fig. 1). At lower altitudes (c. 200 m a.s.l.) there was a plateau with smooth slopes, arid soils and sand deposits dominated by xerophytic vegetation. From 500 to 1400 m a.s.l. the soil types Alfisols and Inceptisols were found (Rodríguez and Mora, 2000), and the vegetation was dominated by ruderal species (weedy colonizers and pioneers on bare or disturbed substrates) and leguminous shrubs. Mean annual temperature ranges from 20 °C at the sea level to 12 °C in the summit area, with several frost events in winter. Annual precipitation varies from 150 mm at lower altitudes to 900 mm at higher areas (Sánchez, 1995).

The road transect in Tenerife ran on the southern leeward slope from sea level to c. 2300 m a.s.l. (Fig. 1). Along this altitudinal gradient the vegetation ranged from coastal halophytic communities, through succulent scrub and xerophytic substitution scrub (up to 800 m a.s.l.), followed by Canarian pine forest at even higher altitudes to high mountain or summit scrub in the Teide National Park. Soils were Litosols at lower altitudes, pumitic soils and Vertisols in some places along the gradient between 800–1400 m a.s.l., and Cambisols at higher altitudes (Rodríguez and Mora, 2000). On the leeward slope mean annual temperature decreases with altitude from 21 °C at sea level to 14.3 °C at 1500 m a.s.l. and to 9.8 °C at 2300 m a.s.l. (Teide National Park). Annual precipitation varies between 130 mm at the coast, 500 mm in areas of pine forest at about 1500 m a.s.l. and below 300 mm in areas above the tree line in the summit scrub (Fernández-Palacios, 1992; Díaz-Díaz et al., 1999). Frost events are common above 1800 m a.s.l. in winter.

Vegetation sampling

In steps of 50 m elevation we located two plots, one each on the two roadsides, starting from the end of the paved or other hard artificial surface of the road. Sites located within villages were not sampled. We sampled 58 (29 altitudinal points) plots in Gran Canaria, and 84 (42 altitudinal points) in Tenerife. The plots were $20 \times 5 \text{ m}^2$ rectangles, with the long axis placed parallel to the road. In each plot we recorded all species of higher plants. Sampling was conducted between October 2004 and March 2005. This period encompasses peak appearance of annuals, since rainfall takes place mostly from late November 2004 to February 2005. Thus, most annual species present in the plots were recorded, including the alien species. Cover of species at ground level was estimated on a scale of 1–10 (corresponding to percent cover classes): 1, traces; 2, <1%; 3, 1–2%; 4, 2–5%; 5, 5–10%; 6, 10–25%; 7, 25–50%; 8, 50–75%; 9, >75%; 10, 100%).

Determination of plot (habitat) characteristics

The altitude of each plot was determined and slope (sexagesimal degrees) was measured with a clinometer. Cover of rock, bare soil, litter and total vegetation were determined as percentages in each plot. We also estimated percent tree canopy cover using a convex spherical densiometer (Lemmon, 1957).

Plot-scale disturbance was classified as (i) mechanical impact by vehicles or pedestrians, (ii) roadside management (residuals of concrete or asphalt, furrows, removal of soil substrate, cleaning of the road shoulder), and (iii) trash dumping. The intensity of these disturbances was estimated using a semi-quantitative scale with the following categories: very high (5), high (4), moderate (3), little (2), and absent (1). The distance to urban nuclei (DUN, in m along roads) was measured as a factor that may represent disturbance intensity and abundance of potential source populations (Rouget and Richardson, 2003). The means of important habitat factors are shown in Table 1.

Species and site characteristics	Gran Canaria	Tenerife	Т	Р
Diversity				
Total species number	21.3 ± 9.9	14.2 ± 9.2	4.4	< 0.001
Species status				
Endemic	5.1 ± 3.3	4.8 ± 2.6	0.6	0.58
Native	8.7 ± 4.1	3.4 ± 3.4	8.4	< 0.001
Introduced	4.0 ± 2.8	3.3 ± 3.6	1.3	0.20
Probably introduced	3.5 ± 2.6	2.7 ± 2.9	1.7	0.09
Total introduced	7.5 ± 4.5	6.0 ± 6.2	1.6	0.11
Life form				
Therophytes	11.0 ± 6.2	7.6 ± 7.6	2.8	0.006
Hemicryptophytes	3.0 ± 1.8	1.5 ± 1.6	5.4	< 0.001
Geophytes	0.8 ± 1.2	0.2 ± 0.5	4.9	< 0.001
Chamaephytes	1.9 + 1.3	1.9 + 1.4	-0.06	0.95
Phanerophytes	4.4 ± 2.2	4.0 ± 2.2	1.2	0.22
Site characteristics				
Slope of terrain ($^{\circ}$)	23.9 ± 17.5	10.6 ± 7.6	6.2	< 0.001
Litter cover (%)	20.0 ± 24.9	29.7 ± 29.1	-2.1	0.041
Total vegetation cover (%)	7.5 ± 1.6	22.6 ± 27.4	-4.2	< 0.001
Bare soil cover (%)	20.3 ± 22.0	14.1 ± 19.8	1.8	0.081
Rock cover (%)	13.5 ± 13.7	19.2 ± 18.9	-2.0	0.050
Canopy cover (%)	15.1 ± 31.0	7.0 ± 13.1	2.1	0.034

Table 1. Species and site characteristics of the roadside transects in Gran Canaria and Tenerife along the altitudinal gradient

Mean number (± 1 SD) of species per plot ($20 \times 5 \text{ m}^2$) is indicated for the different floristic groups. Significant differences between the islands are shown in bold (Student *t* test; df = 140, *P* < 0.05)

Plant species classification

Species were classified according to their status, origin and life form. We distinguished the following four categories: (1) endemics of the Canary Islands; (2) native, non-endemic species; (3) introduced (alien) species; and (4) probably introduced species. This classification is based on recent check-lists for the whole archipelago (Acebes et al., 2004), and for the island of El Hierro (von Gaisberg, 2005; Stierstorfer, 2005; Stierstorfer and von Gaisberg, 2005), which represent the most recently published reports on alien plants of the Canary Islands. Species which were classified as 'possibly native' by Acebes et al. (2004) and 'uncertain' by Stierstorfer and von Gaisberg (2005) were considered native. Generally, for the Canary Islands it is not easy to determine whether a wild species has been introduced by man or reached the area naturally (Stierstorfer and von Gaisberg, 2005).

Naturalized and (potentially) invasive alien species as well as non-endemic, native species were further classified as to their origin or biogeographical affinity and life form - following Kunkel (1991), Hohenester and Welss (1993), Schönfelder and Schönfelder (1997, 2002) and von Gaisberg (2005). We distinguished four different groups of origin: (1) non-European species with a native area outside of Europe; this group included American, African and Asiatic species that were pooled due to low sample sizes (Appendix); (2) Mediterranean species; (3) species with an Atlantic or Eurasiatic distribution (species with an Atlantic-Mediterranean distribution were included in this category): and (4) cosmopolitans, which have a wide geographic distribution and for which the origin is often not known.

Statistical methods

Ordination techniques help in explaining variation in plant communities (Gauch, 1982), and have been used to evaluate trends in plant species composition along spatial gradients (Franklin et al., 1993; Ter Braak and Śmilauer, 1998; Arévalo et al., 1999). As a technique of direct gradient analysis we used partial Detrended Canonical Correspondence Analysis (pDCCA; Hill and Gauch, 1980) in CANOCO (ter Braak and Šmilauer, 1998) to examine how species composition changed along the altitudinal gradient and as a function of the environmental characteristics included in the analysis. Due to differences in species pools and other island characteristics we analysed the data from Gran Canaria and Tenerife separately. We used a forward selection procedure to remove the variables that did not explain a significant portion of the variability reported by the analysis (Monte Carlo permutation test, 500 iterations for P < 0.05). The environmental variables used in the analyses were altitude, slope, the different types of substrate cover, litter cover, canopy cover, overall vegetation cover in the plot, and the three different types of disturbance (see above).

We calculated a correlation matrix of the environmental variables to determine the degree of co-variation between these factors (Pearson correlation coefficients). We performed regression analysis to assess the relationships between species richness in the different plant groups and habitat (plot) characteristics. For altitude, quadratic regression models offered the best fit and highest coefficients of determination. Linear regression models were used for the remaining environmental variables. When altitude was correlated with other environmental factors, we used residuals from linear regression in comparing these factors with altitude to remove the effect of covariation.

Basic statistical methods followed Zar (1984) and were implemented using the SPSS statistical package (SPSS, 1986).

Results

Species origin and life form

In total, 207 and 185 plant species were identified along the roadside gradients in Gran Canaria and Tenerife, respectively (Appendix). The proportion of species with different origin was largely similar on the two islands. We recorded a total of 82 alien species for Gran Canaria (39% of all species) and 69 in Tenerife (38%). Most alien species, i.e. 48 (23%) in Gran Canaria and 38 (21%) in Tenerife, are of confirmed introduced origin. On Tenerife, we found slightly more endemic species along the roads (51; 28% of all species) than on the neighbour island (43; 21% of all species). On Gran Canaria, 82 species (40%) were non-endemic native species and 65 (35%) on Tenerife. The two islands shared only about 46% of the recorded species. The amount of shared species was higher for the alien (53%) than for the native species (41%). On Gran Canaria, the mean number of native non-endemic species per plot was significantly higher than on Tenerife while the two islands differed not in the mean number of species per plot for the endemic and introduced species (Table 1).

Woody species dominated the group of endemic species (86%). Conversely, native non-endemics and introduced species were mostly annual plants. Among the introduced species only 22% were tall-shrubs or trees while 72% were annuals or forbs. On Gran Canaria, we found a significantly higher number of herbaceous species per plot than on Tenerife (Table 1).

Determinants of species richness

Apart from altitude, only distance to the nearest urban areas and litter cover were significantly related to species richness per plot (Table 2). Altitude was the best predictor of species richness per plot in all defined species groups (Table 2). For both islands, species richness showed a unimodal, curvilinear relationship with altitude, irrespective of species status (Fig. 2). The only exceptions were endemic species on Tenerife that showed no significant change in species richness with altitude. Generally, species richness reached a clear maximum at altitudes between 800 and 1000 m a.s.l. Since both categories of introduced species revealed the same distribution pattern on the two islands, we lumped them together. Introduced species were rare below 200 m a.s.l. and almost absent above 1750 m (Fig. 2). Overall, the relationship between altitude and species richness per plot was slightly stronger for the introduced species than for natives (Table 2).

Within both the introduced and non-endemic native species the altitudinal distribution of species richness

changed in relation to their biogeographic affinity (Fig. 3). Non-European species were most abundant at altitudes below 500 m, whereas species of Mediterranean origin peaked at about 900 m, and Atlantic or Eurasiatic species reached the highest number of species per plot only at 1200–1500 m. These patterns were highly consistent among the two islands for both groups of introduced and non-endemic native species, except for non-endemic native Mediterranean species and introduced Atlantic or Eurasiatic species on Gran Canaria. The distribution of cosmopolitan species revealed no significant relations with altitude.

On both islands the number of alien species per plot decreased with distance to the nearest urbanization nuclei (DUN, Fig. 4). Since this factor was positively correlated with altitude on both islands, we used the residuals of a linear regression of DUN on altitude to predict species richness. In the case of Gran Canaria but not for Tenerife, these residuals significantly explained part of the variation in species richness for all species groups (Table 2). Similarly, litter cover or residuals of litter cover were positively related with species richness

Table 2. Coefficients of determination (regression analysis) for number of species per plot in dependence of the three most important environmental variables (we used a forward selection procedure to remove the variables that did not explain a significant portion of the variability in the ordination analysis)

Species group	Tenerife				Gran Canaria				
	Altitude	Res DUN	LitCov	Altitude	Res DUN	Res LitCov			
Endemic species	0.02	0.01	0.04	0.52	0.27	0.23			
Non-endemic native species	0.47	0.17	0.25	0.59	0.27	0.27			
Introduced species (I)	0.48	0.07	0.30	0.28	0.29	0.18			
Probably introduced species (P)	0.43	0.07	0.28	0.72	0.43	0.31			
All introduced species (I+P)	0.49	0.06	0.31	0.60	0.51	0.34			
Total richness	0.50	0.03	0.34	0.73	0.51	0.41			
All introduced species (I+P) (%)									
Non-European origin	0.52	0.14	0.12	0.67	0.03	0.05			
Atlantic or Eurasiatic origin	0.30	0.14	0.14	0.10	0.12	0.09			
Mediterranean origin	0.48	0.09	0.23	0.56	0.36	0.24			
Cosmopolitan	0.19	0.04	0.05	0.16	0.10	0.05			
Non-endemic native species									
Non-European origin	0.81	0.32	0.01	0.78	0.25	0.03			
European origin	0.23	0.10	0.08	0.39	0.02	0.04			
Mediterranean origin	0.37	0.11	0.10	0.05	0.04	0.06			
Cosmopolitan	0.15	0.03	0.24	0.20	0.04	0.00			
Non-endemic native and introduced	species								
Non-European origin	0.84	0.31	0.01	0.86	0.16	0.04			
European origin	0.43	0.20	0.17	0.40	0.07	0.09			
Mediterranean origin	0.65	0.14	0.23	0.30	0.16	0.06			
Cosmopolitan	0.21	0.03	0.15	0.04	0.11	0.04			

Results are shown separately for the different species groups. Significant relationships are given in bold (P<0.05 after Bonferroni corrections). DUN, distance to urban nuclei (km); LitCov, litter cover; Res, residuals from linear regression comparing this factor with altitude to remove the effect of covariation.



Fig. 2. Quadratic regressions of plant species richness per plot on altitude comparing endemic, non-endemic native and introduced species. See Table 2 for regression results.

on Tenerife and Gran Canaria. The proportions of species with different origin were largely unrelated to DUN or litter cover (Table 2). Trash dumping and mechanical disturbance were negatively correlated with altitude on Tenerife, which indicated higher disturbance intensity at lower altitudes and lower intensities at high-altitudes (summit scrub, Teide National Park). Richness of all native (endemic and non-endemic native) species was positively correlated with the richness of all introduced species, even when relationships to important environmental variables (altitude, DUN, litter cover) were statistically controlled (partial correlation: r = 0.31, P = 0.002).

Species composition

The most frequent alien plants shared by the two island roadside transects were *Calendula arvensis*,

Convolvulus althaeoides, Echium plantagineum, Foeniculum vulgare, Galactites tomentosa, Hirschfeldia incana, Sonchus oleraceus and S. tenerrimus. Of these, only F. vulgare is considered a 'transformer' species, i.e. a plant that is able to substantially change the native vegetation landscape (Appendix). Among the species recorded only from the Gran Canaria transect, Dittrichia viscosa and Oxalis pes-caprae were frequent transformers (present in the more humid areas), whereas in Tenerife, Opuntia ficus-indica was the most invasive species albeit mainly on dry areas. Other highly invasive species, such as Agave americana, Opuntia dillenii, Pennisetum setaceum, Ricinus communis, Arundo donax, Nicotiana glauca and Bidens pilosa, are aggressive invaders elsewhere on practically all the Canary Islands, but were detected only in a few plots along the roadside examples. Several alien species were mostly restricted to a clearly defined altitude zone, such as the North-American endemic Eschscholtzia californica to high



Fig. 3. Quadratic regressions of percent alien plant species richness per plot on altitude comparing different species origins. In this case we used percentage instead of number of species because of high between-plot variation in species richness. See Table 2 for regression results.



Fig. 4. Relationship between number of exotic species and distance to urban nuclei (DUN). See Table 2 for regression results.

altitude areas (>1000 m, within the pine forest belt and above) in Tenerife (see Appendix).

For both islands the pDCCA revealed altitude as the most important variable affecting plant species compo-

sition. Altitude was strongly correlated with the first axis (r = 0.98 for Gran Canaria, and r = 0.99) for Tenerife. Trash dumping, mechanical disturbance, other disturbance types and rock cover did not contribute significantly to variation in the analysis (P > 0.05, Fig. 5). The amount of variability explained by the remaining seven environmental variables was significant (F = 1.42, P < 0.05). Intensity of roadside management was also positively correlated with axis II (r = 0.55). Litter cover and slope were also important in the constrained axis I.

Vegetation cover and disturbance through roadside management were also significant explanatory factors. Five environmental variables show no significant variation, i.e. canopy cover, rock cover, mechanical disturbance, litter cover and other disturbance indicators. The remaining six predictors accounted for a significant amount of variation in the analysis (F = 8.35, P < 0.01). Axis II was correlated with bare soil cover and amount of trash on the roadsides (Fig. 5).



Fig. 5. Biplot of the pDCCA for Gran Canaria and Tenerife roadside transects. Eigenvalues: Gran Canaria: axis I = 0.634; axis II = 0.245; cumulative percentage variance explained for species composition: 14.3%; cumulative percentage variance explained for species-environment relationship: 36.1%; Tenerife: axis I = 0.725; axis II = 0.155. Cumulative percentage variances: 12.7% and 38.8%.

Discussion

Altitude-related patterns in the roadside vegetation

Changes in species richness within the groups of different biogeographical status as well as changes in species composition along the altitudinal roadside gradients were consistently similar between Gran Canaria and Tenerife. The only exceptions were the endemic species in Tenerife, which revealed no significant altitudinal pattern. This result suggests that, despite differences in the species pools between the islands, biogeographical patterns in the species distribution along roadsides are consistent along altitudinal transects.

The altitudinal distribution of both alien and native plants in mountain areas is partly related to gradients of environmental stress (Fernández-Palacios, 1992; Alpert et al., 2000; Godfree et al., 2004). Mesic environmental conditions, namely high humidity, low water and thermic stress, and high productivity (Whittaker and Heegaard, 2003) at mid-elevations in the Canary Islands may be the most important factors for peak species richness for both alien and native plants in this zone (unimodal or humped-back curves in Fig. 2). On both islands drought stress increases towards low and high altitudes, and low temperatures are an additional constraint at high altitudes (Fernández-Palacios and de Nicolás, 1995). Both act as filters against the establishment of non-adapted species. These results support the concept of a diversity–productivity relationship (Rosenzweig and Abramsky, 1993), since the combination of hydric and thermic stress limits the availability of resources in the usually nutrient-rich roadside habitats.

Native and alien species responded in a similar way to the altitudinal gradient. Hence, successful establishment of alien species in roadside communities on the Canary Islands seems to be related primarily to elevated resource availability as postulated by the resourceenrichment hypothesis (Davis et al., 2000), but not to competitive interactions or exclusion by native ruderal species as could be expected from the diversityresistance hypothesis (Elton, 1958). The observed positive correlation between alien and native species richness has also been observed in many other studies at different scales (e.g. Lonsdale, 1999; Gilbert and Lechowicz, 2005) and can possibly be explained in the light of the species pool hypothesis (Zobel, 1997; Gilbert and Lechowicz, 2005). In communities which are not saturated due to a limited regional species pool, alien plants with appropriate adaptations to the local environmental conditions may successfully establish and exploit the available resources not fully utilized by the native vegetation. Although all main Canarian ecosystems harbour several native ruderal species with high dispersal capacities that are able to colonize highly disturbed habitats such as roadsides, they can obviously not fully exploit these habitats.

The results of this study also indicate that the observed distribution or realized niches of alien plants along the altitudinal gradient vary in correspondence with the biogeographical affinities and environmental tolerances of the species. Below 1000 m a.s.l. in the frostfree zone, species with a non-European distribution dominated. They originate mostly in tropical and subtropical regions of Africa, Asia or America and are limited by low temperatures. Similar patterns have been found in other areas with a strong altitudinal gradient (Daehler, 2005). Many species seem to profit strongly from good climatic matching in the large subtropical low- to mid-altitude zones of the Canary Islands as several widely invasive alien plants on the Canary Islands, which were also found in our roadside transects belong to this group. These include Agave americana, Eucalyptus globulus, Nicotiana glauca, Opuntia ficusindica, Oxalis pes-caprae and Ricinus communis, which

belong to the 'dirty dozen' of invaders of the Mediterranean islands (Hulme, 2004).

Mediterranean species showed an optimum at midaltitudes (900 m) where a typical Mediterranean climate exists in the south of Tenerife and east of Gran Canaria. Compared to the other two groups, species with an Atlantic or Euroasiatic distribution are more adapted to lower temperatures in winter and less tolerant to long dry periods. In accordance with that, we find their maximum distribution at higher altitudes with at least occasional frost events. The distribution peak of these species was at considerably lower altitudes (1000 m) on Tenerife than on Gran Canaria (1500 m). This difference can be explained by higher anthropogenic influences at high altitudes on Gran Canaria where, no National Park restricts human activities, and by the more humid climate at the surveyed high altitude roadsides on this island.

The role of historic, anthropogenic and natural factors

In general, climatic pre-adaptation of species seems to be an important factor for establishment not only for alien species that reached the islands within the last 500 years in most cases (Parsons, 1981), but also for nonendemic native species that are supposed to have arrived long before without human assistance. Apparently, climatic filters do not only work on 'newcomers', but have also shaped the distribution of non-endemic natives that do not originate in the islands but immigrated over a long period of time by wind, water or birds and reached their climatic equilibrium on each island.

The importance of the biogeographical approach and the species pool hypothesis to plant invasions has been stressed only recently (Gilbert and Lechowicz, 2005; Hierro et al., 2005). Most of the recorded alien species on Gran Canaria and Tenerife are of Mediterranean origin, a pattern that is probably related to the long history of establishment of human settlements, agricultural activity and landscape transformation in midaltitudinal areas since prehistoric times (Parsons, 1981; Aguilera et al., 1994; Naranjo, 1995) which have favoured immigration of this species group. Non-European and Atlantic-Eurasiatic species may be under-represented in the regional exotic species pool also due to historic reasons. If the historic dimension of plant invasion is important, then we might expect an increase of alien plant species in the arid lowlands of the Islands in the future, since human activity has greatly expanded to coastal regions in the last 40 years (Aguilera et al., 1994).

Distance to the nearest urbanization nuclei (DUN) was also a significant predictor for exotic species

richness at roadsides although less important than climatic factors. Road density has increased only recently in low to mid altitudinal zones of the Canary Islands, tightly associated to urban expansion and to the spread of exotic plants. Hence, lower DUN and higher road density can be related to increased 'propagule pressure' which is one of the most important factors explaining richness in alien species invasion success (Wace, 1977; Wester and Juvik, 1983; Turland et al., 1993; Williamson, 1996; Sakai et al., 2001; Scott et al., 2001; Rouget and Richardson, 2003; Dark, 2004; Hulme, 2004; Silva and Smith, 2004).

The negative influence of litter cover on species richness at roadsides is pronounced in the understorey of pine forest in upland regions of the islands where pine needles accumulate and build layers of up to 30 cm which prevent native and alien species from colonizing even roadsides. Hence, the Canarian pine forest, especially the variant on the drier leeward slopes, is characterized by low species diversity (Fernández-Palacios, 1992).

Some differences between the islands in all these relationships were revealed by ordination analysis. While all important factor shaping species distributions were related in Gran Canaria (vectors point in the same direction in multivariate space), for Tenerife several factors had opposite effects (e.g. roadside management and altitude). This finding can be related to the presence of a stronger altitudinal gradient on Tenerife than on Gran Canaria (Fig. 5).

Implications for management

Future attempts to control and manage alien plant species along and across road systems on the higher Canary Islands should focus on the heavily transformed intermediate altitudes, especially in areas close to urbanization nuclei. However, on which altitudes one should concentrate in controlling new populations of alien invasive species might be adjusted according to the different altitudinal distribution patterns of the different biogeographic species groups. Possible measures to reduce propagule pressure and to control invasion along roads are the preferential use of native vegetation in urban and suburban planning as well as planning roads and road network schemes for an increase in utilization by the native and endemic flora (a governmental program to enforce the use of native species and promotion of native species in gardening has been developed in the last years - however, with low impact so far). Further, landscape-level management that reduces disturbance and eradicates alien plants by frequent cleaning may contribute to lower the number of propagules available for plant spread along roads (McNeely, 2000; Forman et al., 2002; Milton, 2003).

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Appendix

List of plant species recorded along the roadside transects on Gran Canaria and Tenerife. Shown are biogeographical status, origin and life form of the species and percentage of plots in which a species was recorded. Transformer species are marked with an asterisk. Status: e, endemic; i, introduced; n, native; p, probably introduced. Origin: end, Canary Islands endemic; mac, Makaronesian region endemic; at, Atlantic; af, African; med, Mediterranean; cosm, cosmopolitan; am, American; euras, Eurasiatic; med atl, Mediterranean–Atlantic; as, Asiatic; med euras, Mediterranean–Eurasiatic. Life form: MPh, Meso- or Megaphanerophyte; NPh, Nanophanerophyte; Th, Therophyte; H, Hemicryptophyte; G, Geophyte; Ch, Chamaephyte. The observed altitudinal range of the species in our survey is indicated in the last four columns (m a.s.l.)

Plant species	Status	Origin	Life	GC n (%)	TF	GC		TF	
			form		(%)	Min	max	min	max
Acacia cyanophylla	i	at	MPh		5			550	800
Adenocarpus foliolosus	e	end	NPh	16	10	480	1680	850	2000
Adenocarpus viscosus	e	end	NPh		24			1200	2300
Aeonium holochrysum	e	end	NPh		1			1000	1000
Aeonium manriqueorum	e	end	NPh	7		260	1640		
Aeonium percarneum	e	end	NPh	33		310	1510		
Aeonium pseudourbicum	e	end	NPh		2			500	1400
Agave americana*	i	am	MPh	7		360	1550		
Agave sp.	i	am	MPh	2		480	480		
Aira caryophyllea	n	eur	Th	2		1680	1680		
Aizoon canariense	n	af	Th	10	12	130	360	100	500
Allium cepa	i	as	G	2		1400	1400		
Allium roseum	n	med	G	12		420	960		
Allium subhirsutum	n	med	G	2		420	420		
Amaranthus cf. viridis	i	cosm	Th	2		270	270		
Amaranthus muricatus	i	am	Th	2		100	100		
Amaranthus sp.	i	am	Th	2		670	670		
Ammoides pusilla	i	med	Th	2		100	100		
Anacyclus radiatus coronatus	n	med	Th		13			1250	1750
Anagallis arvensis	n	cosm	Th	12	8	360	1010	350	1200
Andryala cf. integrifolia	e	end	NPh	2		1400	1400		
Andryala pinnatifida	e	end	NPh	21		360	1550		
Anthoxanthum aristatum	n	med atl	Th	2		1130	1130		
Arenaria leptoclados	n	med	Th		1			1900	1900
Argyranthemum adauctum	e	end	NPh	21		1400	1900		
ssp. canariense									
Argyranthemum frutescens	e	end	NPh		20			150	2000
Argyranthemum gracile	e	end	NPh		1			750	750
Argyranthemum tenerifae	e	end	NPh		11			1850	2300
Arisarum vulgare	n	med	G	16		420	1010		
Aristida adscensionis	n	med	Н		4			850	1050
Artemisia thuscula	e	end	NPh	36	11	130	1510	350	550

Arundo donax*	i	med	Н	3		1180	1400		
Asparagus pastorianus	e	end	NPh	3		360	360		
Asparagus umbellatus	e	end	NPh		1			750	750
Asphodelus aestivus	n	med	G		7			1150	1900
Asphodelus ramosus	n	med	G	24		360	1920		
Asphodelus tenuifolius	n	af	G		2			550	550
Asterolinon linum-stellatum	n	med atl	Th	9		880	1630		
Atalanthus capillaris	e	end	NPh		2			1050	1050
Atalanthus pinnatus	e	end	NPh	5	2	310	1130	450	1000
Atractylis cancellata	n	med	Th	2		480	480		
Atractylis preauxiana	e	end	Ch	2		50	50		
Atriplex glauca	n	af	NPh		6			100	450
Atriplex glauca ssp. ifniensis	n	af	NPh	2		50	50		
Atriplex semibaccata	i	at	Ch	7	4	130	310	400	500
Avena barbata	n	med	Th	10	5	130	1400	1050	1300
Avena fatua	р	cosm	Th	7	1	220	1620	1500	1500
Babcockia platylepis	e	end	Ch	2		1240	1240		
Beta maritima	n	med atl	Н	3		310	310		
Bidens pilosa	i	am	Th		33			500	550
Bituminaria bituminosa	n	med	Ch	48	5	130	1550	400	1700
Brachypodium distachyon	n	med	Th		8			800	2050
Brassica oleracea	i	med atl	Н	7		420	730		
Briza maxima	n	med	Th	3		1630	1680		
Bromus diandrus	n	euras	Th		23			950	1700
Bromus madritensis	р	med atl	Th		12			1050	1750
Bufonia teneriffae	e	end	Ch		4			1900	1950
Bualossoides arvensis	n	med	Th		6			1050	1400
Calendula arvensis	р	med	Th	53	50	220	1680	150	1650
Capsella bursa-pastoris	i	cosm	Th	2	1	1460	1460	900	900
Carduus clavulatus	e	end	Th	5		1020	1240		
Carduus pycnocephalus	n	med	Th	28		360	1770		
Carduus tenuiflorus	n	med	Th		5			1250	1550
Carlina salicifolia	e	end	NPh	9	26	730	1240	700	2050
Carlina xeranthemoides	e	end	NPh		1			2050	2050
Carrichtera annua	n	med	Th		6			550	1300
Carthamus lanatus	p	med	Th	7	1	420	1400	550	550
Castanea sativa	i	as	MPh	9	-	1900	1900		
Cenchrus ciliaris	n	af	Н	10	11	130	360	300	500
Centaurea melitensis	n	med	Th	5	2	360	1680	550	550
Centranthus calcitranae	i	med	Th	3	-	1620	1630	220	220
Cerastium alomeratum	n	cosm	Th	10		1460	1860		
Chamaecytisus palmensis	e	end	NPh	5		960	1400		
Chamaecytisus proliferus	e	end	NPh	9	39	960	1400	1000	2150
Cheilanthes nulchella	n	mac	H	-	2	,000	1100	1900	1950
Cheirolophus canariensis	e	end	NPh		1			500	500
Cheirolophus tevdis	e	end	NPh		4			2000	2050
Chenoleoides tomentosa	n	af	Ch	3	-	50	50	2000	2050
Chenopodium murale	n	cosm	Th	16	2	100	670	1300	1300
Chrysanthemum coronarium	p n	med	Th	5	2	220	310	1500	1500
Cistus monspeliensis	p n	med	NPh	5	12	220	510	850	1400
Cistus symphytifolius	II e	end	NPh		8			1050	2050
Coleostenhus myconis	n	med	Th	7	0	550	1180	1050	2000
Convolvulus althagoidas	i P	med	тн Тh	16	10	<u>⊿</u> 20	1180	550	1350
Convolvulus arvensis	ı n	eliras	H	10	7	720	1100	900	1000
Conveg hongrigensis	11 i	am	Th	5	10	100	270	300	1400
Convza canadansis	1	am	тн Тh	2	10	720	730	500	1400
Cony2u cunuuensis	1	am	1 11	2		/30	730		

Cotula australis	i	af	Th	2		1180	1180		
Crassula tillaea	n	med atl	NPh		4			900	1200
Cuscuta planiflora	n	med	Th		4			300	400
Cynodon dactylon	i	cosm	Н	10		220	360		
Cynosurus echinatus	n	med	Th	9		1240	1470		
Cyperus capitatus	n	med	Н	3		50	50		
Daucus carota	р	med euras	Н	12		1470	1790		
Descurainia bourgeauana	e	end	NPh		11			2050	2300
Dittrichia viscosa*	i	med	NPh	22		130	1520		
Drimia hesperia	e	end	G		4			1150	1400
Drusa glandulosa	n	af	Th	12		480	1240		
Echium bonnetii	e	end	Th	2	2	220	220	800	850
Echium decaisnei	e	end	NPh	9		360	730		
Echium plantagineum	р	med	Th	12	7	480	1400	700	950
Echium wildpretii	e	end	Ch		2			1300	1300
Eragrostis barrelieri	n	med	Th		4			300	400
Erodium botrvs	p	med	Th		5			450	900
Erodium chium	n	med	Th	17	1	220	730	1300	1300
Erodium cicutarium	n	med	Th	36	5	360	1680	400	2050
Erodium malacoides	i	med atl	Th	10	29	130	730	300	1650
Erodium moschatum	n	med atl	Th	7	17	1520	1630	1050	1750
Erucastrum cardaminoides	P n	af	Th	9	1,	670	1130	1050	1750
Ervsimum scongrium	n e	end	Ch	26	10	1400	1900	1700	2300
Eschscholtzia californica	i	am	н	20	8	1400	1700	1250	1400
Escalentus camaldulansis*	i	at	MPh		6			700	800
Eucalyptus camataatensis Eucalyptus alohulus*	1	at	MPh		1			1550	1550
Euclippius giobulus Euchorbia axiaua	n	med atl	Th	2	1	550	550	300	1200
Euphorbia lamarchii		end	NPh	2	10	550	550	300	1200
Euphorbia nenlis	n	cosm	Th	2	17	420	420	500	1200
Euphorbia peplis	;	cosm	Th	2		420	420		
Euphorbia regis-jubag	l n	of	NPh	17		420	1510		
Euphorbia regis-judue	11 n	af	Ch	2		100	100		
Euphorbia segatalis	11 n	an med atl	Th	5	5	100	100	550	800
Euphoroid segerails	n n	med att	TH Th	0	5	360	1470	550	800
Evax pygmaea	p	of	TH Ch	9	12	100	1470	100	550
Fayonia cretica	11	and		24	15	100	420	100	1550
	:	end		29	1	420	260	1550	1050
Files and set a	1	as	MPn Th	2	2	200	200	930	1050
Filago pyramiaata	n	med	In	10	22	1460	1680	500	1 400
Foeniculum vulgare*	1	med		34	23	130	14/0	200	1400
Forsskaolea angustifolia	e	end	Ch	3	21	220	670	500	950
Frankenia laevis	n	med	Ch	0	2	010	1.470	50	100
Fumaria muralis	n	med atl	In	9	2	810	14/0	400	500
Fumaria officinalis	n	euras	In		l			1/00	1/00
Furcraea foetida	1	am	MPh		1		4 6 8 9	700	700
Galactites tomentosa	р	med	Th	43	4	420	1620	500	550
Galium aparine	р	cosm	Th	17	6	670	1550	450	1650
Galium murale	n	med	Th	19		960	1770	1250	1250
Galium parisiense	n	med atl	Th	2		1520	1520	800	800
Galium verrucosum	р	med	Th	21		420	1400		
Geranium dissectum	n	med atl	Th	5		1460	1630		
Geranium molle	n	med atl	Th		1			1250	1250
Geranium purpureum	n	med	Th		1			800	800
Geranium robertianum	n	med atl	Th	9		810	1800		
Geranium rotundifolium	n	med	Th	21		730	1510		
Greenovia aurea	e	end	Ch	2		1240	1240		
Hedypnois cretica	р	med	Th		2			1150	1250

Heliotropium ramosissimum	n	af	Ch	5	5	50	260	50	300
Herniaria cinerea	n	af	Th	2		360	360		
Hirschfeldia incana	р	med	Th	41	17	260	1680	950	1400
Hordeum murinum	i	med	Th		2			1300	1300
Hordeum vulgare	i	cosm	Th		2			1250	1350
Hyparrhenia hirta	n	med	Н	17	21	130	670	300	1050
Hypochoeris glabra	n	med atl	Th	57		310	1680		
Kleinia neriifolia	e	end	NPh	33	24	130	1180	150	1000
Lactuca serriola	i	euras	Th	3	14	1020	1400	550	1750
Lamarckia aurea	n	med	Th		10			900	1350
Lamium amplexicaule	i	euras	Th	9	6	1240	1630	1250	1400
Lathyrus annuus	р	med	Th	12		480	1400		
Lathyrus clymenum	р	med	Th	3		1130	1400		
Lathyrus tingitanus	Ι	med	Th	2	4	1180	1180	1300	1350
Launaea arborescens	n	af	NPh	14	11	50	310	300	750
Launaea nudicaulis	n	af	Th	14		50	420		
Lavandula canariensis	e	end	Ch	2	5	360	360	350	850
Lens culinaris	i	cosm	Th	2		1020	1020		
Leontodon taraxacoides	i	med atl	Th		35			300	1650
Leopoldia comosa	р	med	G	2	1	1800	1800	1150	1150
Lobularia canariensis	e	end	Ch	5	6	670	1240	150	400
Logfia gallica	n	med atl	Th		4			1150	1250
Lolium multiflorum	р	med atl	Н	2		1180	1180		
Lotus campylocladus	e	end	Ch		17			800	2000
Lotus sessilifolius	e	end	Ch		13			50	500
Lycium intricatum	n	med	NPh	2		220	220		
Malva parviflora	р	med	Th	9	18	220	550	100	1350
Marrubium vulgare	i	euras	Н	16		1460	1680		
Matthiola parviflora	n	af	Th		1			1150	1150
Medicago laciniata	р	af	Th		1			700	700
Medicago minima	i	med	Th		33			550	1550
Medicago polymorpha	р	med atl	Th	12	14	310	1130	300	1400
Melilotus indica	i	med	Th		2			1350	1350
Mercurialis annua	р	med atl	Th	2	6	100	100	100	450
Mesembryanthemum crystallinum	i	af	Th	14	8	50	310	100	1300
Mesembryanthemum nodiflorum	i	af	Th	3	5	130	130	50	150
Micromeria benthamii	e	end	Ch	10		1510	1800		
Micromeria varia	e	end	Ch	9	11	670	1130	900	1950
Misopates orontium	n	euras	Th	5	11	670	730	800	1250
Monanthes brachycaulos	e	end	Ch	2		1240	1240		
Moricandia arvensis	i	af	Н	2		360	360		
Nepeta teydea	e	end	Ch		5			2000	2300
Nerium oleander	Ι	med	NPh	3		100	100		
Nicotiana glauca*	i	am	NPh	3	2	50	130	300	550
Notoceras bicorne	n	af	Th		5			1150	1200
Olea europaea ssp. cerasiformis	e	end	MPh	3		730	730		
Ononis diffusa	n	med	Th	5		420	480		
Opuntia dillenii*	i	am	NPh		5			300	950
Opuntia ficus-indica*	i	am	NPh	9	14	220	670	350	1400
Oxalis pes-caprae*	1	af	G	19		360	1020		
Pallenis spinosa	n	med	Th	9	19	550	1470	700	1300
Papaver rhoeas	p	euras	Th	16	1	1130	1550	1300	1300
Papaver somniferum	1	as	Th	-	10			1050	1350
Parentucellia viscosa	n	med atl	Th	2		1020	1020		
Paretaria debilis	n	cosm	Th	9		730	1240		10
Patellifolia patellaris	n	at	Th	26	18	100	670	100	1050

Patellifolia webbiana	n	med	Ch	5		220	480		
Pelargonium sp.	i	af	NPh	3		100	100		
Pennisetum setaceum*	i	af	Н	3	4	310	310	300	550
Pericallis webbii	e	end	Н	26		420	1470		
Periploca laevigata	n	mac	NPh	9	4	310	670	350	800
Phagnalon purpurascens	e	end	Ch	4				550	700
Phagnalon saxatile	n	med	Ch	26	33	260	1400	450	1550
Phoenix canariensis	e	end	MPh	3		100	100		
Picris echioides	Ι	med	Th	2		1020	1020		
Pinus canariensis	e	end	MPh	17	40	1630	1920	1000	2150
Pinus halepensis	i	med	MPh	2		1860	1860		
Piptatherum caerulescens	n	med	Н		15			700	1350
Piptatherum miliaceum	i	med	Н	9	14	130	1680	400	1750
Plantago afra	n	med	Th	-	2	100	1000	1200	1200
Plantago amplexicaulis	n	med	Th		6			1000	1200
Plantago lagonus	n	med	Th	17	20	130	1920	300	1200
Plantago webbii	e	end	Ch	1,	1	150	1720	2250	2250
Plocama pendula	e	end	NPh		1 4			100	450
Pog annua	i	cosm	Th	16	-	1180	1680	100	+30
Polycarnaga divaricata	1	end	NPh	10	1	1100	1000	1250	1250
Polycarpaca nivea	c n	of	NDh	3	1	50	50	1230 50	1230
Polycarpaea nivea	11	al		3 17	1	260	1550	1150	1200
Polycarpon tetraphylium	11	al	111 Th	17	Z	260	260	1150	1200
Polygonum aviculare	1	cosiii		2		500	500		
Polypoaium macaronesicum	11 :	med		2		900	900		
Polypogon monspellensis	1	cosm	In	3		100	100		
Polypogon viridis	n	euras	H	3		100	100	200	200
Portulaca oleracea	1	cosm	Th		l			300	300
Prunus dulcis	1	as	MPh	_	10			800	1400
Pteridium aquilinum	n	cosm	Н	5		1860	1900		
Pterocephalus lasiospermus	e	end	NPh		25			1650	2300
Ranunculus cortusifolius	e	end	Н	19		960	1920		
Raphanus raphanistrum	i	med	Th		5			1250	1350
Reichardia tingitana	n	af	Th		1			1200	1200
Reseda luteola	n	med	Th		1			1300	1300
Reseda scoparia	e	end	NPh		1			350	350
Retama rhodorhizoides	e	end	NPh	3		550	880		
Ricinus communis*	i	af	NPh	2	1	220	220	450	450
Romulea columnae	n	med	G	5		420	1510		
Rubia fruticosa	e	end	NPh	7	2	220	670	700	950
Rumex acetosella	р	cosm	Н	3		1130	1680		
Rumex bucephalophorus	n	med	Th	7		810	1630		
Rumex lunaria	e	end	NPh	22	13	360	1400	400	1200
Rumex vesicarius	n	af	Th	2		550	550		
Salsola kali	n	med	NPh	2		50	50		
Salvia canariensis	e	end	NPh	5		260	360		
Salvia verbenaca	i	med	Th		1			950	950
Sanauisorba meaacarpa	n	mac	Н	2	20	730	730	450	2050
Sanguisorba minor	n	med	Н	3	-•	960	1130		2000
Sideritis kuealeriana	P e	end	Ch	2	4	,000	1120	800	1150
Scandix pecten-veneris	i	med	Th	3	1	730	1400	1350	1350
Schinus molle	i	am	MPh	5	1	750	1100	700	700
Schizoavne sericea	ı n	mac	NPh	2	1 4	50	50	50	300
Scarpiurus muricatus	11 i	med	Th	2	-7 5	550	550	550	1050
Scorpiurus narmiculatus	i	med	Th	3 7	5	180	180	550	1050
Scorphularia alabrata	1	and		2	7	400	+00	1200	2050
Scrophiliana giabraia	с г	mad		1 /	/	120	1550	1200	2050
Seaum rubens	11	mea	111	14		420	1330		

Senecio vulgaris	р	cosm	Th	31	14	670	1550	850	1400
Setaria adherens	i	cosm	Th	5		100	130		
Sherardia arvensis	n	med euras	Th	21		420	1900		
Sideritis cretica	e	end	Ch		4			1450	1750
Sideritis dasygnaphala	e	end	NPh	21		1510	1920		
Silene apetala	n	med	Th		6			900	1250
Silene gallica	р	med	Th		0			800	800
Silene nocturna	p	med	Th		2			1300	1300
Silene tridentata	p	med	Th		2			900	1000
Silene vulgaris	p	euras	Н	40	19	730	1920	850	2050
Sinapis arvensis	i	med euras	Th	3		1130	1180		
Sisymbrium irio	i	med	Th	7	8	100	730	350	1300
Sisymbrium orientale	i	med	Th		4			1300	1400
Solanum nigrum	р	med euras	Th	2		550	550		
Sonchus acaulis	e	end	Н	24		810	1620		
Sonchus canariensis	e	end	NPh		4			1250	1750
Sonchus oleraceus	р	cosm	Th	36	19	100	1510	150	1200
Sonchus tenerrimus	p	med	Th	14	24	100	1180	550	1850
Spartocytisus supranubius	e	end	NPh		6			2250	2300
Spergula arvensis	р	cosm	Th	5	1	1460	1550	850	850
Spergularia fimbriata	n	af	Н	7		100	670		
Stachvs arvensis	n	med atl	Th	10	2	670	1180	800	900
Stellaria media	р	cosm	Th	5		1460	1550		
Stipa capensis	n	af	Th		6			850	1300
Suaeda vermiculata	n	af	NPh	2		260	260		
Taraxacum officinale aga.	р	euras	Th		1			400	400
Teline microphylla	e	end	NPh	43		810	1920		
Theliaonum cvnocrambe	n	med	Th	3		960	1240		
Todaroa aurea	e	end	Н	3		1460	1520		
Todaroa montana	e	end	Н	3		810	880		
Tolpis lagopoda	e	end	Ch	2	7	1240	1240	1250	2050
Tolpis webbii	e	end	Ch		8			2000	2300
Torilis arvensis	n	med	Th	12	2	550	880	850	850
Traaopoaon porrifolius	p	med	Th	2	13	1510	1510	850	1400
Tricholaena teneriffae	n	af	Н	2		310	310		
Trifolium angustifolium	n	med	Th	2		730	730		
Trifolium arvense	n	euras	Th	2	4	730	730	950	1000
Trifolium scabrum	n	med atl	Th		4			700	750
Trifolium suffocatum	i	med atl	Th	2		1400	1400		
Tropaeolum majus	i	am	Th	2		420	420		
Tuberaria guttata	n	med atl	Th	16		810	1800		
Umbilicus aaditanus	n	af	G	19	1	420	1240	800	800
Umbilicus hevlandianus	n	med	Ğ	2		1800	1800		
Urospermum picroides	p	med	Th		12			300	1300
Urtica stachvoides	e	end	Th	2		220	220		
Valantia hispida	n	med	Th	_	2			1200	1250
Veronica arvensis	n	med euras	Th	5	-	1240	1620	1200	1200
Vicia benahalensis	r n	med	Th	U	2	12.10	1020	1350	1350
Vicia disperma	n n	med	Th	29	13	420	1920	1150	1550
Vicia lutea	n	med atl	Th	_,	10		1720	700	1000
Vicia sativa	i	med	Th	2	1	730	730	1350	1350
Volutaria canariensis	e	end	Th	-	1	,20	, 50	1300	1300
Vulpia myuros	n	med atl	Th	26	1	810	1770	1150	1150
Wahlenberaia lobelioides	n	med	Th	20	2	670	670	1200	1250
Zvaonhvllum fontanesii	n	af	NPh	2	1	070	070	50	50
-, gopinymin jonumosu		***			1			20	50

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