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Old-field succession along a precipitation gradient in the semi-arid coastal region of Tenerife

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Abstract

Secondary succession on abandoned fields was studied in the semi-arid region of Tenerife (Canary Islands). At four different sites along a precipitation gradient four chronosequences were sampled. On the whole, 11 fields, abandoned for eight to 70 years, and adjacent near-to-natural stands were studied, with regard to species richness, species composition, vegetation structure, life form distribution and the importance of endemic/exotic species, using uni- and multivariate statistical methods.

In the three drier chronosequences species richness increased significantly during succession whereas in the wettest sequence it peaked very early with a subsequent decline towards the mature stand. Temporal changes in floristic composition were significant and revealed clear directional trends. We could distinguish two pathways of succession: one for the northern coast under more humid conditions and one for the southern coast under arid conditions. Therophytes were generally substituted by nanophanerophytes, while hemicryptophytes and chamaephytes showed low abundances with peaks in late successional stages. At all sites, endemic species replaced exotic species, with regard to both relative number and cover. The relative importance of exotic species in early succession increased with increasing precipitation. Cover of perennials, stand height and stand biomass increased with time since abandonment and water availability. Floristic composition recovered faster than stand structure and, in particular, stand biomass.

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We have the following conclusions (i) The absence of disturbance and in presence of nearto-natural stands in the surroundings, coastal scrub on Tenerife has the capacity to regenerate completely albeit slowly after traditional agricultural use. (ii) The rate and pathway of succession are influenced by site productivity, i.e. mean annual precipitation. (iii) Life form distribution changed in the second phase of succession in relation with the precipitation gradient. (iv) The initially dominant exotic annual plant species seem to be a temporary problem only since, in the course of succession, they are substituted by native perennials. © 2005 Elsevier Ltd. All rights reserved.

Keywords: Secondary succession; Succulent scrub; Canary islands; Chronosequence; Species richness; Biomass; Canonical Correspondence Analysis (CCA)

1. Introduction

Old-field succession is a special case of secondary succession on abandoned, usually arable fields (Glenn-Lewin and Van Der Maarel, 1992). It has been studied extensively in temperate climates (Nicholson and Monk, 1974; Bazzaz, 1975; Bornkamm, 1981; Inouye et al., 1987; Huston and Smith, 1987; Tilman, 1987; Osbornová et al., 1990; Myster and Pickett, 1994; Meiners et al., 2002) as well as under Mediterranean conditions (Houssard et al., 1980; Tatoni et al., 1994). In semiarid to arid regions, however, studies on secondary succession are rather scarce (Cox and Madrigal, 1988; McLendon and Redente, 1992; Stylinski and Allen, 1999; Wezel and Böcker, 1999; Bolling and Walker, 2000, Bonet 2004), possibly because succession proceeds very slowly under these harsh conditions (Dean and Milton, 1995; Cody, 2000).

Most of the studies focused on successional changes in one region, analysing a single chronosequence or data from permanent plots. Often, only the chronosequence approach (space-for-time substitution, Pickett, 1989) is possible, since data from long-term permanent plots are extremely rare. Although space-for-time substitution has some disadvantages such as possible small differences between the plots with regard to site history, edaphic and microclimatic conditions or availability of propagules (Pickett, 1989; Bakker et al., 1996), it has been shown, however, that the approach is basically sound (Debussche et al., 1996; Foster and Tilman, 2000).

As already mentioned by Prach (1993), there is a considerable lack of knowledge concerning the relationship between the dynamics of secondary succession and environmental factors. This relationship can be studied by comparing successional series from habitats with different site conditions, which can be established experimentally, for instance by adding nutrients (Tilman, 1987; McLendon and Redente, 1992). Alternatively, larger geographical regions have to be taken into account which, however, makes comparisons more difficult (Prach, 1993; Prach et al., 2001).

In this context, site productivity has been found to influence the rate of succession as well as changes in species richness and structural parameters (Tilman, 1987; Prach, 1993). Models predict an asymptotical increase in species richness during succession under very harsh environmental conditions (Osbornová et al., 1990; Peet, 1992), while improved productivity, i.e. water availability in semi-arid regions, leads to a maximum of species richness in an early or intermediate stage of succession with a subsequent decline to stabilization (Horn, 1981; Tatoni et al., 1994; Bonet, 2004). Also species interactions are expected to change in relation with the increase of environmental stress (Bertness and Callaway, 1994). Therefore, comparative studies of environmental gradients and succession could help to identify the more general patterns of successional change and to evaluate existing succession models and the recent ecological theory (Prach, 1993; Peet, 1992; Bruno et al., 2003).

On Tenerife, strong environmental gradients occur over short distances (Fernández-Palacios and de Nicolás, 1995), e.g. with regard to precipitation. The precipitation gradient affects also the coastal region where succulent scrub represents the potential natural vegetation. This provides an excellent opportunity for studying how precipitation affects secondary succession towards succulent scrub. In the past 50 years, the coastal landscape on Tenerife has changed dramatically: many formerly cultivated areas were abandoned due to socio-economic changes, while many natural stands of succulent scrub have been destroyed by touristic developments and modern agriculture. Although many successional stages of succulent scrub have been described phytosociologically (Rivas Martínez et al., 1993; Rodríguez Delgado et al., 1991), the successional process in relation to precipitation has, up to now, never been investigated in detail.

Save for precipitation, site conditions were very similar on all the abandoned fields selected for the present study. Further, all of them remained undisturbed after abandonment and they were adjacent to near-to-pristine stands of succulent shrub. In this study, therefore, the limitations of the chronosequence approach were minimal.

This paper deals with the secondary succession on abandoned fields in the semiarid coastal region on Tenerife, covering a precipitation gradient from 96 to 300 mm per year. Specifically, our objectives were: (1) to analyse the successional changes in vegetation structure and floristic composition, with special regard to life form types and exotic species, (2) to elucidate how precipitation affects successional change, (3) to discuss the results with emphasis on existing succession models and the recent ecological theory including species interactions and (4) to reveal the consequences for nature conservation and restoration management.

2. Study area

Tenerife is the largest (2034 km²) and tallest (3718 m a.s.l.) island in the Canary Archipelago which is located in the northern Atlantic (27–29° north latitude and 13–18° West longitude). Climate and vegetation vary considerably with both altitude and exposure to the prevailing trade-winds (Fernández-Palacios, 1992) which result in steep ecological gradients (Fernández-Palacios and de Nicolás, 1995). Since the main mountain chain runs east–west the north-east trade winds bring more humidity

to the northern or windward slope than to the more arid southern or leeward slope (Table 1).

This precipitation gradient also affects the coastal areas (Otto et al., 2001), where all four study sites were established within a range of 100 km: 1 = Punta del Sol (north), 2 = Teno Bajo (west), 3 = Güímar (south-east) and <math>4 = Rasca (south, Table 1). Mean annual precipitation ranges from 300 mm at Punta del Sol to only 96 mm at Rasca, the southern most part of the island. This arid to semi-arid subtropical climate is characterized by a pronounced dry season from May to September with almost no rainfall and a wet season from October to April. Precipitation and the relative humidity of the air decrease towards the south, while the duration of sunshine, radiation and evaporation increase (Höllermann, 1982). Mean annual temperature varies between 19.3 at Punta del Sol and 21.8 °C at Rasca, whereas daily and seasonal fluctuations of temperature range from 6 to 8 °C for all study sites. Meteorological data were taken from nearby stations.

Tenerife is a volcanic island with the oldest material dated 11.6 Ma (Ancochea et al., 1990). At all four study sites the parent material is formed by basaltic lava flows of the third geological series, ranging in age from 0.01 to 0.5 Ma, save for the Malpaís de Güímar where the substrate is less than 10.000 years old. The soils in the semi-arid coastal regions are usually, very poorly developed skeletal soils (lithosols, at Punta del Sol and Güímar), or soils with a more or less marked clay-enriched

Site characteristics	Chronosequence						
	1	2	3	4			
Site name	Punta del Sol	Teno Bajo	Güímar	Rasca			
Number of old fields	4	3	2	2			
Number of replicates	3	3	3	3			
Age of old fields (year)	8, 20, 50, 70	20, 30, 60	25, 50	35, 60			
Distance to mature stand (in 100 m)	3, 1.75, 2.5, 2	2, 1.5, 0.5	2, 2	1.5, 1.5			
Last crop before abandoned	b, b, w, w,	t, t, w	t, w	t, w			
w = wheat, b = banana, t = tomato							
Mean annual precipitation (mm)	300	250	180	96			
Mean annual temperature (°C)	19.3	20	19.6	21.8			
Type of substrate	Basaltic lava	Basaltic lava	Basaltic lava	Basaltic lava			
Age of substrate (Ma)	0.25	0.25	0.01	0.25			
Soil type of undisturbed site	Lithosol	Aridisol	Lithosol	Aridisol			
Altitude (m a.s.l.)	50	120	90	20			
Slope (°)	5	10	5	5			
Exposition	NW	NW	SE	S			
No. of species in local species pool	88	75	65	56			
No. of exotic species in local species pool	41	27	23	12			
Percentage of exotic species (%)	46.6	36.0	35.4	21.4			

 Table 1

 Site characteristics and chronosequences

horizon (aridisols, at Teno Bajo and Rasca) (Fernández-Caldas et al., 1982). All sites are located between 20 and 120 m a.s.l. and show slope inclinations of $5-10^{\circ}$. Since all the selected sites are part of protected areas, they remained undisturbed save for occasional light grazing by goats. Since grazing intensity was very low in the last 50 years for all sites, this management factor was not considered in the analysis.

Succulent scrub is an open shrub vegetation adapted to the subtropical semi-arid climate of the coastal region, dominated by stem succulents of the genus *Euphorbia* and leaf succulents or sclerophyllous shrubs that grow up to 4 m tall (Rivas Martínez et al., 1993). Most abundant species are the cactus-like *Euphorbia canariensis* L. the hemispherical shaped *E. balsamifera* Ait. and the umbrella-shaped *E. obtusifolia* Poir. which form different types of the so called cardonal-tabaibal. Nomenclature of vascular plant species follows Hansen and Sunding (1993).

3. Methods

3.1. Sampling design

In the coastal zone of Tenerife, four areas were chosen, covering together the whole precipitation gradient. In each area, a varying number of successional stages (2–4) of different ages were selected and compared with the near-to-natural vegetation in the immediate surroundings (<300 m distance) never used for agriculture. On the whole, we studied four near-to-natural stands and 11 old fields, abandoned between 8 and 70 years ago, using a total of 45 plots. Because of the rectangular shape and relative small size of the fields, we sampled each successional stage with three plots, each 10×10 m in size and 50 m apart, leaving sufficient distance to the edge of the field in order to avoid edge effects. We made sure that all the elements of a chronosequence were very similar with regard to site conditions and management history.

Management history and the date of abandonment were reconstructed by studying five series of aerial photographs from 1952 to 1995 and by interviewing land owners. On all the fields abandoned first (>50 years ago), the last crop was wheat, whereas on the fields abandoned more recently (<50 years ago), the last crops consisted of irrigated banana plantation at Punta del Sol in the north or irrigated tomato plantation at the three other sites. Soils of cultivated terraces were usually enriched with fine earth collected in adjacent areas.

Cover, height, biovolume and biomass were measured for all individuals of all perennial vascular plant species (>30 cm) between January 1994 and May 1997. Above-ground biomass was estimated with help of the indirect dimensional method (Whittaker and Marks, 1975), a non-destructive approach based on experimentally established allometric regression equations linking biovolume and dry weight of individual plants (Otto et al., 2001). Cover of annual species was visually estimated, biomass calculated based on equations established for the most abundant annuals. Stand height is represented as the mean value of the 10 tallest shrubs.

3.2. Data analysis

Temporal changes in floristic composition were analysed using Detrended Correspondence Analysis with detrending by segments (DCA, Hill, 1979; CANOCO package, ter Braak and Šmilauer, 1998). For ordinations, cover values were log transformed. To evaluate the importance of the factor time we ran canonical correspondence analysis (CCA) with time as the only environmental factor. Monte Carlo permutation test was applied to determine the significance of the axes (1000 permutations). CCA ordination with six exploratory variables was used to visualize the relationships between floristic composition and the two overlapping gradients (time and precipitation). Forward selection procedure by means of a Monte Carlo permutation test was carried out to test the significance of the variables. Time since abandonment was grouped in seven age classes, each covering a 10-year period, and an additional class eight for the near-to-natural mature stands (>70 year). Mean annual precipitation, mean annual temperature and altitude were included as continuous variables, exposition and substrate age as dummy variables.

Plant species were categorized with respect to life form (Raunkiaer, 1934) and origin (Lems, 1960). With regard to life form we distinguished therophytes, hemicryptophytes, geophytes, chamaephytes and nanophanerophytes, with regard to origin endemic, native/non-endemic and introduced species.

Significance of differences between successional stages within a chronosequence and between sites within a certain successional stage (early = therophyte stage, eight to 35 years abandoned, late = advanced stages, 50 to 60 years abandoned, mature = near-to-natural stand) was tested with the non-parametric Kruskal Wallis test. For the comparison of exotic and native species pools we used the nonparametric Mann-Whitney test. We followed the statistical procedures of Zar (1984) using the SPSS statistical package (Anon., 1990). The following index was chosen to measure species turnover between successional stages:

$$T = (J + D)/(S1 + S2),$$

where J = number of species which immigrated between successional stages I and II, D = number of species which disappeared between successional stages I and II, S1 = total number of species in successional stage I, S2 = total number of species in successional stage II. With exception of DCA ordination, we displayed only the centroids or the mean values, respectively, of the three replicates for each successional stage in order to simplify the figures. Successional species were defined as species which did not appear in the mature stand (non-climax species). Early and late successional species are exclusive to the respective stage only.

4. Results

4.1. Changes in species richness and floristic composition

In the 45 plots studied, a total of 169 species of vascular plants were found; 41.4% of them were exotic. At the three drier sites (site 2, 3 and 4), total species number as

well as the numbers of annuals and perennials increased with both time after abandonment and increasing precipitation reaching their maximum in the mature stands (Fig. 1). Differences between abandonment ages were mostly significant, differences between chronosequences resulted not significant (Table 5). Generally, the increases were more pronounced for the perennial species. At the wettest site, in contrast, total species number decreased significantly during succession from 40 in the 8th year to only 17 species/100 m² in the mature stand implying a very fast increase in the first 7 years. The marked subsequent decrease is mainly due to a decrease in the number of annuals but also the number of perennials does not peak at the mature stage.

DCA-ordination of all four sites and all 45 plots showed clearly two directions of succession (Fig. 2). The most humid chronosequence 1 is mainly related to the first axis ($\lambda_1 = 0.741$) with a direction from left to right, whereas the drier chronosequences two, three and four are primarily related to the second axis ($\lambda_2 = 0.259$) showing trajectories from bottom to top. The first two axes accounted for 22.0% of the variance in the species data. The distances between plots in the ordination diagram indicate that, with the exception of site Rasca, species exchange was faster in the first 50–60 years, i.e. from the initial to the advanced stages, and that the advanced successional stages were floristically already very similar to the mature stands. We also can observe a tendency of the trajectories in direction of the centre of the ordination diagram in the second phase of succession which represents a process of convergence of successional pathways probably caused by the dominance of the spurge shrubs.



Fig. 1. Changes of species richness and vegetation structure with time since abandonment. Differences between successional stages within each chronosequence were analysed with the non-parametric Kruskal-Wallis test (* = p < 0.05, m = mature stand).



Fig. 2. DCA ordination including all four chronosequences (all 45 plots) with the first two axes ($\lambda_1 = 0.741$, $\lambda_2 = 0.259$) which explained 22.0% of the variance in the species data (S1–S4 = successional stages, m = mature stand, time since abandonment in brackets).

Monte Carlo permutation test for the unique axis ($\lambda_1 = 0.551$) of the CCA ordination with time as the only exploratory variable was highly significant (p < 0.005). CCA ordination with six site variables and 15 centroids of replicates is presented in Fig. 3. The second axis ($\lambda_2 = 0.556$) showed a strong correlation with time since abandonment while the first axis ($\lambda_1 = 0.662$, p < 0.01) represented a climatic gradient with mean annual precipitation, mean annual temperature and exposition (north/south) as most important factors (Table 4). Although precipitation and temperature resulted to be correlated in the coastal region on Tenerife (Otto et al., 2001), temperature as well as exposition were significant variables after testing by the forward selection procedure (Table 4). The third axis ($\lambda_3 = 0.358$) was related to substrate age. The CCA-biplot (Fig. 3) represents parallel successional pathways in relation to the two gradients (precipitation and time). The first two axes accounted for 35.5% variance in the species data and 60% variance of the species-environment relation. The restricted inertia of the data set was 2.328, the unrestricted 3.434.

The early successional stages were generally dominated by introduced (*Mesembryanthemum crystallinum* L., *M. nodiflorum* L., *Patellifolia patellaris* (Moq).S., F.-L., et W.) or native, non-endemic annuals (*Spergularia fallax* Lowe,



Fig. 3. CCA ordination including all four chronosequences (centroids of replicates) and six exploratory variables with the first two axes ($\lambda_1 = 0.662$, $\lambda_2 = 0.556$) which explained 35.5% of the variance in the species data. Centroids of the dummy variables are represented with a cross, other variables with an arrow (S1–S4 = successional stages 1–4, m = mature stand).

Aizoon canariense L.) in the south and exotic annuals (*Chenopodium murale* L., *Calendula arvensis* L., *Torilis arvensis* (Schult.) Thell., *Mercurialis annua* L., *Nicotiana paniculata* L. and *Parietaria debilis* Forst. fil.) in the north. *Volutaria canariensis* Wagenitz and *Ammodaucus leucotrichus* Coss. et Dur. ssp. *nanocarpus* Beltrán were the only endemic annuals that were locally frequent in the south. At Punta del Sol only, the perennial grasses *Hyparrhenia hirta* (L.) Stapf and *Cenchrus ciliaris* L. covered 10–20% of the understory in the 20–70year-old stages.

The first colonizing woody species are usually endemic or native, non-endemic shrubs with a wide ecological amplitude and a certain ruderal character. Artemisia thuscula Cav., Rumex lunaria L., Argyranthemum frutescens (L.) Sch. Bip. and Lavandula multifida (L.) ssp. canariensis (Mill.) P. et. P. occurred in the north, while Schizogyne sericea (L. fil.) DC., Launaea arborescens (Batt.) Murb. and Lycium intricatum Boiss. were more frequent in the south. These species form a transition shrub stage (matorral de sustitución, Rodríguez Delgado et al., 1991) between the therophyte stage and the first Euphorbia-stage. E. obtusifolia was generally the first spurge shrub that invaded the abandoned fields. In the chronosequences one, two and four E. obtusifolia was subsequently substituted by E. canariensis and/or E. balsamifera. At Punta del Sol, we found an additional stage with deciduous shrubs

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like *Periploca laevigata* Ait. and *Rubia fruticosa* Ait. between the first and second *Euphorbia*-stage.

4.2. Successional species and species turn over

At the most humid site (chronosequence 1), 70.5% of all species that appeared in the chronosequence were successional species not present in the mature stand (Table 2). Most of them were annuals, growing only in the youngest stages. At the most arid site (chronosequence 4), in contrast, we recorded only 18.2% successional species and most of them were perennials occurring in the late successional stage (60 years abandoned) only. Chronosequences two and three had intermediate positions with 28% and 30% successional species, respectively. Calculations of species turnover confirm these observations (Table 3). Turnover was clearly higher in the first phase between early and late successional stages for the two more humid sites one and two. The opposite was true for the most arid site, where turnover was higher in the second phase of succession (60 year to mature stand). Site three showed an intermediate position with similar turnover rates for both phases. The overall turnover rates between early succession and mature stands were surprisingly similar in all four chronosequences (Table 3). In terms of the numbers of species which immigrated and disappeared, however, species exchange differed quite substantially between the four chronosequences: with increasing precipitation the numbers of exchanged and disappeared species increased whereas the number of successful immigrants was high at sites two, three and four and quite low at site one. At arid sites, therefore, the successional process was characterized by species accumulation as opposed to species elimination—by a few highly competitive perennials—on the most humid site (Table 4).

4.3. Changes in vegetation structure and life form distribution

In all four chronosequences, cover of perennial species as well as stand height and biomass increased significantly during succession, with maximum values in the

Successional species in the chronosequence (% species of the local species pool which did not appear in the mature stand (non-climax-species), early and late successional species are restricted to the respective

Successional species (in % of local species pool)	Chronosequence					
	1	2	3	4		
Successional species	70.5	28.0	30.2	18.2		
Successional annuals	45.5	16.0	23.8	7.3		
Successional perennials	25.0	12.0	6.3	10.9		
Early successional species	44.3	14.7	15.9	7.3		
Late successional species	10.2	12.0	6.3	10.9		

Table 2

successional stage only)

Table 3

Turnover rate between successional stages (e = early successional stage, l = late successional stage, m = mature stand, l = highest value, 0 = lowest value)

	Chronosequence											
	1		2		3		4					
	e-l	l-m	e-m	e-l	l-m	e-m	e-l	l-m	e-m	e-l	l-m	e-m
Turnover rate	0.64	0.44	0.63	0.62	0.23	0.62	0.55	0.47	0.66	0.33	0.42	0.63
Immigrating species	19	6	13	35	14	38	18	22	32	12	24	35
Disappearing species	43	20	51	13	10	13	14	13	15	3	6	5
Exchanged species	62	26	64	48	24	51	32	35	47	15	30	40

Table 4 Importance of exploratory variables in CCA-analysis

Variable	<i>p</i> -value	Variance explained	Axis 1	Axis 2	Axis 3
Time since abandonment	0.001	0.55	-0.1559	-0.9541	0.1219
Mean annual precipitation	0.002	0.55	-0.7501	0.3764	-0.1811
North/south-exposition	0.005	0.36	-0.5875	0.2457	-0.5069
Mean annual temperature	0.015	0.32	0.6711	-0.3085	-0.181
Altitude	0.091	0.25	-0.0447	-0.3065	-0.142
Substrate age	0.123	0.21	-0.1726	0.1137	-0.7618

p-value and variance explained by each variable obtained by forward selection procedure by means of Monte Carlo permutation test, and correlations of variables with the first three ordination axes.

mature stands (Fig. 1). Cover of annuals, in contrast, decreased dramatically. In the most humid chronosequence one, we found high cover values of perennials already at a young successional stage (20 year) where stratified shrub vegetation had grown. Subsequently, the cover of perennials decreased slightly, probably due to gaps with stony surfaces originating possibly from a washout of the top-soil and from fallen terrace walls. In the near-to-natural mature stand the cumulative cover of perennials attained more than 100%. Stand height, cover of perennials and stand biomass differed significantly between the chronosequences (Table 5). After 50–60 years of abandonment, these variables reached in chronosequence one already 73%, 68% and 25%, respectively, of the values observed in the adjacent near-to-natural mature stands, whereas in chronosequence four we recorded much lower values (50%, 28% and 11%, respectively) (Fig. 4).

Relative species number and relative cover of the different life forms changed also significantly with time since abandonment (Fig. 5). In the course of succession, therophytes were substituted primarily by nanophanerophytes but also by geophytes and hemicryptophytes, both with regard to relative species number and relative cover. The relative species number of hemicryptophytes increased significantly with Table 5

Differences between chronosequences within successional stages (early = therophyte stage, 8-35 years abandoned, late = advanced stages, 50-60 years abandoned, mature = near-to-natural stand) with regard to several vegetation characteristics tested by the non-parametric Kruskal-Wallis test

Vegetation characteristics	Successional stage					
	Early	Late	Mature			
Species richness						
No. all species*	_	_	_			
No. annuals*	_	_	_			
No. perennials*	-	_	+			
Exotic/endemic species						
No. endemic species*	_	_	+			
No. exotic species*	_	+	_			
Relative No. endemic species	+	-	_			
Relative No. exotic species	+	_	_			
Relative cover endemic species	+	+	_			
Relative cover exotic species	_	_	+			
Ratio exotic/native species	+	_	_			
Ratio exotic/native annuals	+	-	_			
Life forms						
Relative No. annuals	+	_	+			
Relative No. hemicryptophytes	_	_	_			
Relative No. geophytes	_	_	_			
Relative No. chamaephytes	+	+	+			
Relative No. nanophanerophytes	_	+	+			
Relative cover annuals	_	+	+			
Relative cover hemicryptophytes	_	+	+			
Relative cover geophytes	_	+	+			
Relative cover chamaephytes	_	+	+			
Relative cover nanophanerophytes	_	+	+			
Structure						
Stand height	+	+	+			
Cover of perennials	+	+	+			
Stand biomass	_	+	+			

+ = significant difference, p < 0.05;— = not significant, * = difference tested only for the group of sites 2, 3 and 4.

the time since abandonment whereas their relative covers peaked (15–20%) in intermediate to late successional stages. Among the hemicryptophytes, only native, non-endemic perennial grasses reached higher abundances. The relative species number of the geophytes increased significantly during succession. Their relative cover, however, remained always very low, and in chronosequence 4, representing the most arid site, this life form was not present at all. Chamaephytes revealed no clear successional trends. Differences in relative cover of life forms between chronosequences resulted significant in late successional stages and mature stands (Table 5). In general, nanophanerophytes and geophytes showed higher abundances,



Fig. 4. Life form composition of the native and exotic species pool.



Fig. 5. Changes of the importance of life forms with time since abandonment. Differences between successional stages within each chronosequence were analysed with the non-parametric Kruskal-Wallis test (* = p < 0.05, m = mature stand).

therophytes and chamaephytes lower abundances in the moist north than in the dry south.

4.4. Importance of exotic species

The regional exotic species pool (all chronosequences, Fig. 4) is clearly dominated by therophytes (87%), which, in the regional native species pool, attain only 40%.

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With respect to the local species pools, the percentage of therophytes was significantly higher in the introduced than in the native species pool, the percentage of chamaephytes and nanophanerophytes significantly lower (Mann-Whitney test, p < 0.05). The native species pools (local and regional) contain many more woody species. In fact, there are very few introduced woody species (*Opuntia dillenii* (Ker-Gawl.) Haw., *O. ficus-barbarica* A. Berger, *N. glauca* Grah., *Agave americana* L. all of American origin) that invaded the old fields.

With increasing time since abandonment, the relative importance of the endemic species increased markedly and significantly with regard to both species number and cover, whereas the relative cover of the exotic species decreased from about 90% to less than 10% for all sites (Fig. 6). Fig. 6 shows a clear positive correlation between mean annual rainfall and the time after abandonment when the relative cover of the exotic annuals started to decrease. With respect to the relative number of species, the decline was more pronounced in the north than in the south (Table 5, Fig. 6). The ratio of exotic/native species in the early successional stage differed significantly between sites (Table 5). We found three times more exotic than native species at the most humid site, while the contrary was found at the driest site where the number of native species is twice the number of exotic species. At sites two and three, the ratio was 1.5 and 1, respectively. The late successional stages and the mature stands, however, showed very similar percentages of exotic species at all sites, and, consequently, differences between chronosequences were not significant. The ratio exotic/native annuals followed the same trend although the differences between sites are smaller indicating that, within the group of therophytes, species exchange and substitution of exotic by native annuals also occur (Table 5). The presence of introduced species in the local species pool seemed to be related to the water availability of the site, since we recorded much higher values at the most humid site (Table 1). The absolute number of introduced species found per 100 m^2 decreased strongly with time only in chronosequence one, while it increased slowly or staved stable in the other chronosequences (Fig. 6).

5. Discussion

5.1. Species richness

Most of the studies about old-field succession report that species richness increased with increasing time since abandonment (Bazzaz, 1975; Hard, 1976; Schmidt, 1981; Bornkamm, 1981; Inouye et al., 1987; Tilman, 1987). This increase can be more or less continuous with a maximum either at the end of succession (Nicholson and Monk, 1974) or in an intermediate phase followed by a slight decline and a subsequent stabilization towards more mature stages (Houssard et al., 1980; Tatoni et al., 1994). Models predict an asymptotical increase in species number during succession under very harsh environmental conditions leading to equilibrium between immigration and extinction (Osbornová et al., 1990; Peet, 1992). With improved water availability species number increases rapidly after abandonment due



Fig. 6. Changes of the importance of endemic and exotic species with time since abandonment. Differences between successional stages within each chronosequence were analysed with the non-parametric Kruskal-Wallis test (* = p < 0.05, m = mature stand).

to the combination of abundant resources and lack of competition, reaching a maximum already at some intermediate stage of succession (Horn, 1981; Brown and Southwood, 1987). At the end of succession, the more competitive species dominate and displace the early successional species leading to a decline in diversity (Grime, 1979).

Species richness pattern during old-field succession in the area of succulent scrub on Tenerife show both tendencies mentioned above along the existing precipitation gradient: in case of the three drier chronosequences species number increased throughout the whole observation period while it peaked very quickly after abandonment at the most humid study area, Punta del Sol, at the north shore. At Punta del Sol, the decrease in species number started already 8 years after abandonment and was entirely due to a drop in the number of annuals, most likely caused by the rapid increase in stand height as well as number and cover of perennials. About 50 years after abandonment also the number of perennials started to decline, concomitant with a steep increase in stand biomass supporting the idea that competition for soil water and the reduction of regeneration niches become more important in the late phase of succession.

In chronosequence one, the last crop and related soil conditions differed in function of the time of abandonment, which may also have influenced our findings. But, overall, the faster increase of species richness at this site can probably be attributed to climatic factors. Very similar results were reported from semi-arid Mediterranean old fields (Bonet, 2004), where species richness maximum occurred 10 years after abandonment with a subsequent decline. Mean annual precipitation in that study area reached 302 mm, mean annual temperature 18.2 °C, which is comparable to the climatic conditions at Punta del Sol.

5.2. Floristic composition and vegetation structure

DCA ordination showed two main pathways of succession related to water availability and possibly also the type of last crop. The fields of the three drier chronosequences were last cultivated with tomatoes and irrigated with slightly salty water which, together with the high evaporation rate in the semi-arid climate, could have increased the salt concentration in the top soil. This could explain the great floristic similarity of the initial stages at sites two, three and four dominated by the salt-tolerant Mesembryanthemum species. At Punta del Sol, the most humid of the four chronosequences studied, by contrast, the last crop was banana. It has already been stressed that differences in site history may influence successional patterns (Inouye et al., 1987; Pickett, 1989). Previous cropping can affect cover of the most abundant species following abandonment (Bonet 2004). The advanced successional stages were floristically already very similar to the near-to-natural mature stands whose species composition was found to depend primarily on the plant-available soil water (Otto et al., 2001). Consequently, the last crop influences species composition only at the beginning of succession, whereas during the later phases of succession the water supply seems to be crucial.

The general sequence of life form substitution is: therophytes—perennial grasses nanophanerophytes. An interesting observation is that the initial therophyte stage lasted 5–10 years in the north but more than 30 years in the south. Most likely, this time-lag was caused by the differences in rainfall and thus water supply. Possibly it may have been prolonged by the presence of *M. crystallinum*, an aggressive exotic species known to inhibit the growth of other ephemeral and perennial species on degraded pastures at the coast of California (Vivrette and Muller, 1977). The establishment of the first individuals of *Euphorbia* species on *Mesembryanthemum* dominated fields at Teno Bajo within 30 years after abandonment suggests that this inhibiting factor is not that important in the coastal region of Tenerife.

In the study area, the hemicryptophyte stage, characteristic of secondary succession in more temperate climates (Grime, 1979; Schmidt, 1981; Brown and Southwood, 1987; Tatoni et al., 1994) is represented only by perennial grasses. Perennial forbs are generally rare in the succulent scrub and were not observed to play a major role during succession. Chamaephytes showed low abundances during succession and did not become dominant in any of the chronosequences.

In agreement with the high percentage of nanophanerophytes in the native species pool, this life form dominated the later successional stages and the mature stands. Shrubs with a more ruderal life strategy could be distinguished from typical late successional species. Among the three abundant stem succulent *Euphorbia* species, *E. obtusifolia* showed a clear ruderal character with rapid growth, abundant seed production but low competitive ability. The cactus-like *E. canariensis*, on the other hand, was observed to colonize the abandoned fields very late with very small individuals, due to a very slow growth and possibly also to other reproductive characteristics such as low seed production and germination rate. *E. canariensis*, is apparently very tolerant to water stress and—in the absence of mechanical disturbances—also highly competitive. The third species, *E. balsamifera*, has an intermediate strategy (Otto, 2003).

Species turnover and the magnitude of species exchange during secondary succession in the coastal region of Tenerife seemed to be influenced by water availability. In the arid south of the island, species were accumulated rather than exchanged. In the humid north, on the other hand, the succession was primarily characterized by elimination, with a few highly competitive perennials eliminating most of the annuals. In the arid south, only few species are able to grow under the extreme edaphic and microclimatic conditions on freshly abandoned fields. But once a species is successfully established, it normally can persist for a long time. For the chronosequences studied in the arid south with mean annual precipitation ranging from 96 to 250 mm, concepts such as facilitation by other species (Connell and Slatyer, 1977; Bruno et al., 2003) correspond better to the observed dynamic patterns than the species replacement model (Horn, 1981). Facilitation is especially important where environmental stress is strong as e.g. in very arid regions (Franco and Nobel, 1989). For the coastal scrub in the Canary Islands Mies and Aschan (1995) have already demonstrated how the dominant shrubs affect the microclimatic conditions. We assume, therefore, that facilitations play an important role not only in mature stands but also in old-field succession. Where vegetation cover closes rapidly, such as

observed in the most humid chronosequence one with a mean annual rainfall of 300 mm, competition-free niches for colonizing plants become rare (Harper, 1977; Grime, 1979). Under more humid conditions, therefore, concepts such as the initial floristic composition (Egler, 1954) or the competition sorting model (Horn, 1981) seem to be more important for interpreting the observed successional processes.

In case of the more humid chronosequences one and two, species turnover was observed to be highest at the beginning, followed by a decline in the course of succession. This trend of a declining species turnover with advancing succession has been documented in many studies in temperate regions (Bornkamm, 1981; Pickett, 1982; Prach, 1993; Myster and Pickett, 1994). The phenomenon is usually attributed to species-specific differences in growth rate, life history and longevity (Grime, 1979; Huston and Smith, 1987; Foster and Tilman, 2000). At the drier sites, species turnover was more constant over time, supporting the findings from other succession studies in extreme environments (e.g. Sarmiento et al., 2003). Turnover rates during succession have been related to climatic conditions (Shugart and Hett, 1973; Bornkamm, 1981; Myster and Pickett, 1994), to nutrient supply (Inouye et al., 1987; Tilman, 1987; McLendon and Redente, 1992) or both (Osbornová et al., 1990), i.e. to factors affecting site productivity. Not only species exchange, but also changes in vegetation structure during secondary succession have been described to be related to site productivity. Where nitrogen is the primary limiting soil nutrient, plant cover and biomass was found to depend on nitrogen supply (Inouve et al., 1987; Tilman, 1987). In the semi-arid coastal regions of Tenerife soil water was observed to be the limiting factor (Otto et al., 2001), whereas nutrients were not limited in young successional stages (Rodríguez Rodríguez et al., 2002). Consequently, the differences in structural parameters between the chronosequences seem to depend here mainly on water supply.

5.3. Exotic species and regeneration

In all the chronosequences studied, the relative cover of introduced species, mainly annuals, was found to be important only in the initial stage of succession. Later they were substituted by endemic and native species. This replacement process seems to be a general trait of secondary succession related to disturbance and life history traits of the invading species (Inouye et al., 1987; Foster and Tilman, 2000; Meiners et al., 2002). In our study it was much more pronounced in the humid north, where the percentage of exotic species dropped from 70% to 30% in the course of succession, than in the south with a drop, at Rasca, from 32% to 20%. This supports the idea that the invasibility of ecosystems is also related to site productivity (Inouye et al., 1987; Loope, 1992; Sobrino et al., 2002). Considering landscape level, exotic species play an important role in the overall species pool persisting in the mosaic of different successional stages.

Soil degradation has also been reported to influence native species recovery during secondary succession (Stylinski and Allen, 1999; Bolling and Walker, 2000). In this study, traditionally cultivated soils have not been altered in a way that would prevent the recovery of the endemic vegetation. But soil conditions certainly change

in old-field succession as reported from soil analysis of different successional stages of coastal scrub on Tenerife (Rodríguez Rodríguez et al., 2002).

Otto et al. (2001) reported that disturbed sites in the coastal region of Tenerife can be dominated by exotic perennials such as Opuntia dillenii, O. ficus-barbarica and Agave americana. These exotic perennials have similar life strategies as the native *Euphorbia* species but with the additional advantages of protective spines and highly effective vegetative reproduction. In the present study, O. dillenii was found only at Teno Bajo, with a cover of up to 5% in the advanced successional stages and up to 1% in the adjacent natural stands. This suggests that in the absence of disturbance native Euphorbia shrubs are much more competitive than the above-mentioned exotic perennials. Another aggressive invader of African origin, the perennial grass Pennisetum setaceum, was only found in the earliest succession stages at Punta del Sol and only with few individuals. This species should be monitored, however, since locally it caused real problems both on the Canary Islands as well as on Hawaii (Hughes et al., 1991; García-Gallo et al., 1999). The low number of exotic perennials in the coastal scrub of Tenerife can probably be explained: 1) by the existence of endemic ruderal shrub species such as Schizogyne sericea, Artemisia thuscula or R. lunaria that fill the ecological niche and 2) by the still low number of introduced shrub species adapted to the arid environment in the regional species pool. Species of African origin such as L. arborescens and L. intricatum abundant in successional stages are assumed to have reached the Canary Islands without the help of man and are, therefore, considered to be native.

6. Conclusions

In natural stands of succulent scrub in the coastal region of Tenerife, floristic variation was found to be strongly related to precipitation (Otto et al., 2001). The present study showed that precipitation controls not only site productivity and floristic composition of the near-to-natural vegetation but also speed and course of succession on abandoned fields. At the northern, more humid coast, species turnover is higher at the beginning of succession and more species are exchanged during succession, while in the arid south species are rather accumulated than exchanged and turnover is more constant. Our findings are, therefore, consistent with the reports of other authors who found that rate of succession and recovery time are very slow where environmental stress is strong and productivity is low (Shugart and Hett, 1973; Burrows, 1990; Osbornová et al., 1990; Peet, 1992; Dean and Milton, 1995).

With respect to floristic and structural composition we propose here, for the first time for succulent scrub on Tenerife, two different successional pathways: the pathway north where structural recovery is fast and high vegetation cover and high biomass accumulation can lead, in addition to below-ground competition for water, also to above-ground competition for light (competition sorting model, Horn, 1981), and the pathway south where strong environmental stress slows down the processes of structural regeneration and the successful establishment of a few adapted species leading to a step-by-step colonization (facilitation model, Connell and Slatyer, 1977; facilitative succession, Bruno et al., 2003). These findings would support the idea that with the increase of environmental stress the importance of competition decreases as facilitation increases (Bertness and Callaway, 1994).

During succession, the relative cover of exotic species, decreased from about 90% in the earliest stages to insignificant levels (<10%) in the near-to-natural mature stands. At none of the four chronosequences studied, did exotic plants alter the course of succession. The invasion by exotic annuals on recently abandoned fields seems to be related here not only to disturbance but also to site productivity (Inouye et al., 1987).

Even though our results suggest that—in the absence of disturbance and in presence of near-to-natural stands in the surroundings—succulent scrub is able to regenerate completely albeit slowly on abandoned fields, we should not forget that, on Tenerife, this endemic vegetation type is still being destroyed at a considerable rate, and that better protection is more than urgent.

Nomenclature: Hansen and Sunding (1993).

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