ORIGINAL ARTICLE

Compositional and structural differences in two laurel forest stands (windward and leeward) on Tenerife, Canary Islands

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Abstract The laurel forest of Anaga is the most emblematic community of the Canarian Archipelago. Restoration programs are being developed to increase laurel forest area on the island of Tenerife. Structural and spatial characteristics determine many aspects of the community, including regeneration patterns, disturbance level, stand history. In spite of the importance of this information for restoration, few quantitative studies have been conducted on laurel forest dynamics. We analyzed two stands of the Anaga laurel forest of different aspect. The main difference between the two sites was the wind exposure, one leeward and the other windward. Regeneration, spatial distribution of regeneration, tree species composition, asexual regeneration and environmental parameters were analyzed in three 50×50 m plots at each site. Both sites differ in important aspects such as species richness, species composition, asexual regeneration and dead tree composition, while they are not different in basal area, density, density of regeneration and density of dead trees. Both sites have had similar management in the last century. Asexual regeneration is able to maintain the present species composition, while sexual regeneration is able to offer future changes in the canopy composition. Regeneration strategies and the effect of some environmental characteristics should be considered in restoration programs.

Keywords Basal area · Density · Regeneration · Spatial distribution · Wind exposure

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Introduction

Comparative studies on similar ecosystems of different regions of the world have been carried out from various points of view (Ovington 1983; van der Maarel 1996; Ohsawa 1999). At a local scale, topographical as well as edaphic habitat conditions are decisive factors in determining the types of formation and the local plant community, since these factors modify environmental conditions, affecting colonization and potential persistence for some species (Hugget 1995). Structural and spatial characteristics determine many aspects of the community, including regeneration patterns, disturbances level, stand history (Moeur 1993; Arévalo and Fernández-Palacios 2005).

Species composition of forest stands is dependent on many factors (e.g., environmental characteristics, species relationships, disturbances); however, stand history can be considered one of the most important factors in populated areas or near population centers due to the traditional use of forest resources by man (Oliver and Larson 1976). The laurel forest of the Canary Islands is considered the most emblematic ecosystem of the archipelago (Santos 1990). However, few quantitative studies have revealed relevant aspects of its dynamics (Fernández-Palacios and Arévalo 1998; Arévalo et al. 1999, 2008; Ohsawa et al. 1999; Shumiya et al. 1999). Understanding ecological processes of the community is one of the most important goals for laurel forest management since laurel forest restoration is increasingly supported by the Canarian society. Lack of acknowledgment of ecological processes increases the possibility of unsuccessful restoration programs.

The aim of our work was to reveal the effects of aspect on two laurel forest stands of Anaga. We evaluated the

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hypothesis that aspect has an effect on species composition, regeneration, mortality and spatial distribution of regeneration. An understanding of the dynamics of the forest, including its variability due to environmental factors, could become a useful tool in the management of this protected area. Such results could be important for the specific and correct design of restoration programs especially in those areas where all the laurel forest has disappeared due to human activities in the last four centuries.

Materials and methods

Study site

The study was conducted in the Anaga Rural Park in the northeast corner of Tenerife, Canary Islands (28°19'N, 16°34'W). The park encompasses a 7- to 8-million-yearold basaltic massif (Ancochea et al. 1990) covering some 130 km². The park represents 7% of Tenerife's total area. We selected two sites in the park as representing the bestconserved laurel forests of Anaga: El Moquinal on the windward slope (elevation 775-850 m) and Aguirre (elevation 810-925 m) on the leeward slope. Tenerife's evergreen laurel forest has been extensively exploited since the arrival of Europeans in the fifteenth century (Parsons 1981). Today, only 10% of the forest remains, and it has been formally protected since 1988, currently experiencing fewer human disturbances and no area reduction. No data are available about the precise forest age, but aerial photographs from 1952 show the forest in its current state, in terms of both extent and physiognomy. In the 1940s, there was still some illegal, small-scale forest exploitation due to its protection schedule and public character (Fig. 1).

The annual precipitation of the park reaches 900 mm, but can be twice this amount taking into account fog drip (Kämmer 1974). The mean annual temperature is close to 15°C with minimal annual and daily fluctuations. There are no frost events. Two seasons can be differentiated, winter and summer, but in most years differences between the two most extreme months are not large (differences between the averages of the extreme months: 8°C, 5% relative humidity and 100 mm of rain) (Ceballos and Ortuño 1977). The soils have been classified in the order Entisol, suborder Orthens, being typical of high slope areas. They maintain a high grade of humidity due to the hydrate aluminum silicates, and have a thick A horizon (Fernández-Caldas et al. 1985). The content in organic matter is high ($\sim 10\%$) and pH is around 5.5 (Fernández-Palacios and Arévalo 1998).

The yearly as well as the daily variations of wind speed are affected by both the large-scale and the local

conditions, but yearly variations are usually indicative of the regional climatology. The Canary Islands, situated in the Trade Wind Belts, show a maximum during the summer months, as compared with most areas in northern Europe, which have a minimum in the same months (Petersen 1989). Persistent north-east trade winds predominate in summer (90–95%) and are less frequent in winter (50%).

The canopy height of Anaga's laurel forest is 10–20 m, depending on the slope. Maximum heights are found at basin bottoms decreasing progressively towards the basin borders. The laurel forest of Anaga contains a total of 19 tree species (Santos 1990). Dominant species include *Laurus azorica*, *Erica scoparia*, *Erica arborea*, *Ilex canariensis*, *Prunus lusitanica*, *Myrica faya* and *Viburnum tinus*. The dominance of a given species depends on site conditions. For example, *E. scoparia* dominates in forest ridges, *L. azorica* in mesic zones and *E. arborea* in more disturbed areas (Anon 1973). Further information on stand composition, structure and environment in the study sites can be found in Fernández-Palacios et al. (1992), Arévalo and Fernández-Palacios (1998, 2000, 2007) and Arévalo et al. (1999).



Fig. 1 Present (*shaded*) and historical (enclosed in the *dotted line*) distribution of the laurel forest on Tenerife

Sampling design

Between June and September 1999, we randomly selected three 2,500 m² square plots (50 \times 50 m) in each of the two sites (respectively, windward and leeward) with different altitude and aspect (plots 1–3 were in El Moquinal and plots 4–6 in Aguirre). In each plot, we noted Universal Transverse Mercator (UTM) coordinates, aspect, wind aspect, altitude, slope, and measured canopy cover percentage (using a convex spherical densiometer; Lemmon 1957), understory cover, rock, litter and soil cover (percentages) (Table 1). Species nomenclature follows Hansen and Sunding (1985).

We defined "trees" as stems of at least 2.5 cm dbh (diameter at breast height), "saplings" as stems taller than 50 cm and less than 2.5 cm dbh of sexual origin, and "suckers" as sapling-size stems of asexual origin (connections with parent stems, with some exceptions, were apparent). We did not take into account saplings shorter than 50 cm because their high rate of germination and death. Previous studies recommended these classes in agreement with the physiognomy and phenology of this forest (Fernández-Palacios and Arévalo 1998). In each plot, we mapped all saplings (with an accuracy of 0.05 m). In each plot, basal area and density for living and dead trees as well as sucker and sapling densities were recorded per species (Table 2).

In order to determine the composition of the seed bank, five randomly located samples per plot, comprising 3 kg of the first 5 cm of soil, were taken from the study sites and set to germinate under greenhouse conditions. The soil samples were placed in 5-cm-deep and 40×55 -cm quadrangular plastic trays that were irrigated daily with distilled water. Three additional trays filled with sterilized soil were used as controls in order to determine the seed rain existing in the greenhouse. Emerging seedlings were allowed to grow until identified, and then removed.

Statistical analysis

We compared altitude, slope, basal area of trees, density of trees, sapling density, sucker density and basal area and density of dead tree between windward and leeward plots using the Student's *t* test (P < 0.05).

We studied the spatial distribution of sapling Laurus azorica and Viburnum tinus (these two species comprise more than 90% of the total sexual regeneration) in plots with more than ten stems, using the univariate $K_1(t)$ function, which is the expected number of other individuals within a distance, t, of any individual (Ripley 1977). We tested the spatial distribution for each meter to a distance of 21 m. This analysis is effective in detecting spatial relations between points on a map (Bailey and Gatrell 1995) and is recommended when information of multiple neighbor (closest regenerative stems to each other) distances are available (Busing 1996). The null hypothesis is the complete randomness of spatial distribution of stems of one species for $K_1(t)$. Because a minimum-maximum number of stems are required for carrying out these analyses, the number of plots in which we ran the analysis differs for the different species.

For a graphical representation, we used the transformation of the $K_1(t)$ function to the $W_1(t)$ function proposed by Szwagrzyk (1992) and Szwagrzyk and Czerwczak (1993). This graphical display allowed us to visualize in just one curve which of the values of the index at different distances differed from a random spatial distribution (for P < 0.05). When the spatial distribution of the stem at the given distance does not differ from a random distribution, the value of the curve at that distance is zero. When significant aggregation is detected, the values of the curve are positive (the value will increase depending on the differences among the expected values and observed values). Negative values of the curve indicate significant repulsion at the given distance. Due to

Table 1 Some environmental and biotic characteristics of the sampled plots (slope measured in sexagesimal degrees)

Variable	El Moquinal 1	El Moquinal 2	El Moquinal 3	Aguirre 1	Aguirre 2	Aguirre 3
UTM (28RCS) coordinates	7,192/5,714	724/5,750	7,217/5,767	7,610/5,655	7,605/5,710	7,550/5,670
Sampling date	May 1999	June 1999	July 1999	May 1999	July 1999	September 1999
Altitude (m)	775	850	820	850	925	810
Exposure	NNE	WNW	NW	SE	S	S
Wind exposure	Windward	Windward	Windward	Leeward	Leeward	Leeward
Slope (°)	15	10	30	20	40	30
Understory cover (%)	15	20	15	40	60	45
Canopy cover (%)	90	95	95	95	95	95
Soil cover (%)	5	10	10	10	5	15
Rock cover (%)	1	5	5	1	10	15
Tree species richness	9	7	8	13	12	11

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	Living	g trees	Dead	trees	Living	trees	Dead	trees	Living	trees	Dead 1	rees	Living t	rees	Dead tr	ees	Living	trees	Dead t	rees	Living	tre	ses
	Ba	Dens	Ba	Dens	Ba	Dens	Ba	Dens	Ba	Dens	Ba	Dens	Ba	Dens	Ba I	Dens	Ba	Dens	Ba	Dens	Ba	De	su
Apollonias barbujana	I	ļ	I	I	I	I	I	ļ	I	I	I	I	1.09	116	0.22 4	0†	I	ļ	I	I	1.83	108	
Erica arborea	3.03	92	I	I	1.68	44	0.01	4	13.05	584	0.15	24	14.90	772	1.24	356	0.87	52	0.00	4	2.93	128	
Erica scoparia	0.67	44	0.01	8	1.59	128	Ι	I	1.70	188	0.14	24	1.30	152	1.96	200	3.11	276	0.67	124	7.89	792	
Heberdenia excelsa	I	I	I	I	I	I	I	I	I	I	I	I	3.35	332	0.09	12	14.38	632	0.67	56	0.02	×	
llex canariensis	5.60	1.23	0.11	48	10.34	1.26	0.05	24	7.58	1.06	0.07	28	3.38	496	0.26 8	88	3.83	308	0.29	24	4.93	444	
llex perado	1.98	108	I	I	I	I	Ι	I	0.72	36	Ι	I	I	I			I	I	I	I	I	Ι	
Laurus azorica	7.16	1.23	0.55	268	5.43	832	0.10	28	3.82	456	0.66	88	7.96	628	2.54	284	8.13	792	2.06	380	8.67	1.03	
Myrica faya	5.21	108	0.12	8	2.70	92	0.21	12	2.64	52	0.04	4	9.49	276	1.09	96	5.41	144	0.29	32	10.77	280	
Ocotea foetens	I	I	I	I	I	I	I	I	I	I	I	I	I	I			0.01	4	I	I	I	I	
Persea indica	I	I	I	I	Ι	I	I	I	I	I	Ι	I	0.08	4			0.08	4	I	I	0.69	32	
Picconia excelsa	I	I	I	I	Ι	I	I	I	Ι	I	I	I	0.54	12			1.93	20	I	I	0.01	8	
Prunus lusitanica	13.72	1.84	1.16	356	11.81	1.5	0.13	40	8.43	728	I	I	2.75	140			7.60	700	0.84	188	I	I	
Rhamnus glandulosa	I	I	I	I	I	I	I	I	I	I	I	I	1.01	36			1.62	40	I	I	66.0	32	
Viburnum tinus	0.14	96	0.01	8	0.16	112	I	I	0.84	88	0.35	40	0.27	148	0.06	28	1.51	240	0.07	20	0.43	200	
Visnea mocanera	I	I	I	I	I	I	I	I	I	I	I	I	0.24	32	, 1		I	Т	I	I	Т	I	
Total per plot	37.51	4.74	1.96	969	33.71	3.97	0.5	108	38.78	3.19	1.41	208	45.27	3.03	7.24	1,404	48.48	3.21	4.89	828	37.33	2,950	

the multiple comparisons, Szwagrzyk (1992) suggested considering as significant aggregations of dispersion just when values are greater than 1 or less than -1 in the $W_1(t)$ display graph.

We used ordination techniques to explain patterns of community variation (Gauch 1982). We applied detrended correspondence analysis (DCA; Hill and Gauch 1980) to analyze tree species composition of the plots. We also included other categories apart species richness as dead tree composition, sapling composition, sucker composition and seed bank composition in the analysis. The centroids for El Moquinal and Aguirre (using coordinates for the plots at each site with the different categories) are shown in the graph.

We performed all multivariate analyses with the CA-NOCO package (ter Braak and Šmilauer 1998). Basic statistical methods were followed as given in Zar (1984) and were applied using the SPSS statistical package (SPSS 1986).

Results

Environmental differences between plots at windward and leeward sites were not significant for the parameters analyzed (altitude, slope, understory cover, canopy cover, rock cover and soil cover). Thus, we can assume that wind exposure is the main difference between the two sites (Table 1).

Species richness was higher in Aguirre. El Moquinal was dominated mainly by *Prunus lusitanica*, while Aguirre had different dominant species in each plot. The density of dead trees was higher significantly at Aguirre (900 ind/ha), with *Erica scoparia*, *Erica arborea* and *Myrica faya* being the dominant species of dead trees (Table 2). The number of dead trees is related to the species composition dominance, with dominant dead trees *L. azorica* and *P. lusitanica* in El Moquinal and *L. azorica* and *E. scoparia* in Aguirre (Table 2). Viburnum tinus and *Laurus azorica* were the dominant species of saplings in El Moquinal, but there was high variability in dominance in Aguirre plots (Table 3). Seed banks were dominated in all of the plots by pioneer species (*E. arborea* and *E. scoparia*) (Table 3).

No significant differences among biotic parameters (basal area, trees density, saplings density, suckers density and dead trees basal area and density) were detected (for P < 0.05). Saplings were much more abundant in El Moquinal plots, but there was also a high variability among them, preventing significant differences (Fig. 2).

The spatial distribution of regeneration showed mainly aggregation at all analyzed distances for *Laurus azorica* and *Viburnum tinus* (*V. tinus* was not analyzed in El

Moquinal 2 because the high number of saplings did not allow the use of the analysis). In the case of *Laurus azorica*, only plot Aguirre 1 showed significant differences from a random distribution at all distances, while the other plots had a Wt value below 1, indicating no significant differences with respect to a random distribution. Aggregation was stronger for *V. tinus*, with significant aggregations for all plots after 3 m (except in plot Aguirre 1, which showed no significant differences from a random distribution for any of the given distances) (Fig. 3).

The DCA for the plots using the species densities at different categories (live trees, dead trees, saplings, suckers and seed bank composition) was graphically displayed. Figure 4 shows the categories per plot coordinates in axes I and II of the DCA. Axis I clearly separates sapling and seed bank composition from live tree, dead tree and sucker composition. Axis II separates El Moquinal plots from Aguirre plots in the last three categories. Dead trees and suckers of El Moquinal were closely related to the live tree plots of Moquinal, and similar results were obtained for Aguirre. Figure 5 shows the DCA species coordinates. Sapling composition was more characterized by Viburnum tinus. Prunus lusitanica, Ilex perado and I. canariensis were more related to the El Moquinal plots, while Laurus azorica and Apollonias barbujana were more related to the Aguirre plots. For seed bank composition, a high relationship was found in both sites with Erica arborea, E. scoparia and Teline canariensis. Dead trees in Aguirre were primarily Laurus azorica and Myrica faya. Dead trees in El Moquinal plots were more similar to the live tree composition, except for plot 3, with some mortality of Laurus azorica, making its location closer to that species' coordinates. Similarities between dead tree and live tree composition in Aguirre are weaker.

Figure 5 also indicates the centroids for El Moquinal and Aguirre, calculated as the average of the Euclidian distance among all the parameters of each site (coordinates of live trees, dead trees, sucker, saplings and seed bank germination).

Discussion

The laurel forest of Anaga has been considered highly variable with respect to species composition and species richness. Environmental variability and stand history are two characteristics recognized as very important in determining species composition (Fernández-Palacios and Arévalo 1998; Ohsawa et al. 1999). The analysis of this variability should help to understand the conservation status of the Anaga forest.

El Moquinal, on the windward slope of Anaga, is a forest dominated by *Prunus lusitanica*. This species

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	Sap	Suck	Sbank	Sap	Suck	Sbank	Sap	Suck	Sbank	Sap	Suck	Sbank	Sap	Suck	Sbank	Sap	Suck	Sbank
Apollonias barbujana	ļ	I	I	I	I	I	I	I	I	1,120	924	I	20	172	I	60	116	
Erica arborea	4	I	259	I	I	75	I	4	162	I	4	17	I	I	1	I	I	21
Erica scoparia	I	I	276	4	12	7	I	4	10	I	I	293	I	I	13	I	I	22
Heberdenia excelsa	8	I	I	I	I	I	I	I	I	108	120	I	624	I	I	40	I	I
llex canariensis	40	320	I	12	644	I	12	836	I	24	168	I	4	152	I	16	128	I
llex perado	I	224	I	I	I	I	68	116	I	I	I	I	I	I	I	I	I	I
Laurus azorica	92	1,148	I	124	1,168	I	256	1,464	I	628	1,052	I	328	2.18	I	120	2,072	I
Myrica faya	4	100	15	I	48	I	24	44	1	I	136	I	4	48	8	I	64	2
Ocotea foetens	I	I	I	I	I	I	I	I	I	I	I	Ι	Ι	I	I	I	I	Ι
Persea indica	I	I	I	Ι	I	I	I	I	I	1	I	Ι	I	8	I	I	I	Ι
Picconia excelsa	I	I	I	I	I	I	I	I	I	1	8	I	16	I	I	36	I	I
Prunus lusitanica	I	1,112	I	52	4,012	I	4	2,084	I	I	260	I	I	1,324	I	I	56	I
Rhamnus glandulosa	I	I	I	I	I	I	I	I	I	10	I	Ι	20	I	2	68	I	I
Teline canariensis	I	I	I	I	I	I	I	I	I	I	I	4	I	I	2	I	I	I
Viburnum tinus	1,492	408	I	14,028	876	I	3,388	296	I	31	156	2	288	260	I	792	212	I
Visnea mocanera	I	I	I	I	I	I	I	I	I	1	8	Ι	I	I	I	I	I	I
Total per plot	1.64	3,312	551	14.22	6.76	82	3,752	4,848	173	804	1,912	316	1,284	3,972	26	1,072	2,532	45



Fig. 2 a Mean basal area (m^2/ha) for live and dead trees in the Aguirre and Moquinal sites. b Densities (ind/ha) of trees, dead trees, saplings and suckers

regenerates mainly by asexual regeneration (remnant regeneration strategy; Fernández-Palacios and Arévalo 1998), which is very uncommon in other laurel forest stands, even on the same island. Aguirre, dominated in some areas by shade-intolerant species such as Myrica faya, Erica scoparia and E. arborea (pioneer regeneration strategy; Fernández-Palacios and Arévalo 1998), has higher species richness than El Moquinal (12 species on average, while El Moquinal has 8 species on average). This indicates that environmental conditions in Aguirre are not allowing the development of a mesic laurel forest. Leeward orientation offers more environmental variability, thus improving the possibility for the establishment of more species with different regeneration strategies. Both stands are considered mature stands (Arévalo et al. 1999), and differences can be attributed to environmental variability.

The spatial distribution of *Laurus azorica* and *Viburnum tinus* regeneration showed similar patterns at both sites. For both species, aggregation was detected more consistently after 7–8 m, but not in all plots. This could be related to the shade-tolerant regeneration strategy of both species, which makes the establishment of both species possible in patches where environmental conditions are adequate. At short distances, there is no aggregation, and also, especially for



Fig. 3 Values of the Wt index for the saplings of **a** *Laurus azorica* and **b** *Viburnum tinus* in the El Moquinal and Aguirre plots. The index was calculated every meter to 21 m (in plot El Moquinal 2, there were not enough data to calculate the index for *V. tinus*)

Viburnum tinus, there is a less intense aggregation after 14 m. This could be considered due more to environmental conditions than the influence of biotic relationships (Arévalo and Fernández-Palacios 2007). These two species accounted for 90% of the sexual regeneration at both sites. The lack of differences between sites (El Moquinal and Aguirre) can be extrapolated from the spatial distribution of saplings.

The ordination analysis revealed similarities between sexual regeneration of the sites. However, some characteristics were specific for each site. El Moquinal was dominated by *Viburnum tinus*, and Aguirre by *Apollonias barbujana* and *Hebernia excelsa*. Suckers, dead trees and live trees were segregated, depending on whether they had a leeward or windward exposure. For Aguirre, shadeintolerant species (*Myrica faya*) were more abundant in the dead tree category. *Laurus azorica* was a very common species in all the plots and categories, thus it was not discriminated by axis I and axis II of the DCA. Suckers were strongly related to canopy composition in both sites. For the seed bank composition, shade intolerant species (*Erica arborea, E. scoparia* and *Teline*

DCA - coordinates for plots categories



Fig. 4 DCA axes I and II and category coordinates. *tree* live trees, *sap* saplings, *dead* dead trees, *su* suckers, *seed* seed germination. *M* Moquinal, *A* Aguirre, followed by *numbers* indicating the number of the plot at each site



Fig. 5 DCA axis I and II species coordinates. Apba, Apollonias barbujana; Erar, Erica arborea; Ersc, Erica scoparia; Heex, Herberdenia excelsa; Ilca, Ilex canariensis; Ilpe, Ilex perado; Laaz, Laurus azorica; Myfa, Myrica faya; Ocfo, Ocotea foetens; Pein, Persea indica; Piex, Picconia excelsa; Prlu, Prunus lusitanica; Rhgl, Rhamnus glandulosa; Teca, Teline canariensis; Vimo, Visnea mocanera; Viti, Viburnum tinus. The centroids for both sites, El Moquinal and Aguirre, are also shown

canariensis) were dominant at both sites, showing a lack of relationship between seed bank and canopy composition (Fig. 5).

Wind orientation is an important factor in the dynamics of the laurel forest of Anaga, determining species composition, asexual regeneration and dead tree composition, but having a minor effect on sapling composition and seed bank composition. Also, wind orientation determines the successional status of the stands. Conditions on the leeward (Aguirre) side allow a higher density of shade-intolerant species that are more restricted on the windward (El Moquinal) face. Asexual regeneration is able to maintain species composition at each site; however, sexual regeneration could produce future changes in species composition if environmental conditions remain similar (Arévalo et al. 1999). Spatial relationships in Anaga have been previously analyzed in other studies (Arévalo and Fernández-Palacios 2005), and they reveal how the spatial distribution of trees is related to the high rate of asexual regeneration, showing aggregation to 2-3 m for all the tree species analyzed. Suckers remain near the adult trees, having a high spatial association at short distances. Almost all the tree species in the laurel forest are able to regenerate asexually, increasing the possibility of maintaining the present species richness.

The laurel forest of Tenerife has been well conserved in the last century and has experienced an important recovery in the last 20 years (Wildpret and del Arco 1999). Understanding differences among stands through monitoring (Thomas and Palmer 2007) could help to design species restoration programs in areas where the laurel forest has been eliminated.

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