

# **Regeneration strategies of tree species in the laurel forest of Tenerife (The Canary Islands)**

José María Fernández-Palacios & José Ramón Arévalo\*

Departamento de Ecología, Universidad de La Laguna, 38206 La Laguna, Tenerife, Islas Canarias, Spain; (Temporary address: Department of Botany, Oklahoma State University, Stillwater, OK 74078, USA)

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### Abstract

The laurel-forest of the Canary Islands is a montane cloud-forest. In order to gain some knowledge on the processes that maintain tree species diversity, we conducted an analysis of three different laurel-forest plots of the Anaga massif (Tenerife), varying in canopy composition but growing under similar environmental conditions. For each plot we recorded basal area of the canopy trees (h > 1.30 m), the density of suckers and seedlings (h < 1.30 m), as well as seed-bank composition. The plots have similar regeneration composition, which appears to be independent of differences in canopy composition. *Laurus azorica* is the most common seedling species, whereas *Prunus lusitanica* is the most abundant species among suckers and basal shoots. Neither *Erica arborea* nor *Myrica faya*, the two main canopy trees in one of the plots, were found in any of the stands as seedlings or suckers, despite their existence as viable seeds in the seed-bank. The regeneration composition and the canopy composition in one of the plots is remarkable different, revealing differents dynamics processes in the three plots. The results suggest the existence of three well-defined ecological groups: pioneer (regeneration primarily by seedlings), non-pioneer (regeneration by seedlings and suckers) and remnant species (regeneration primarily by suckers). These three groups and the effect of small scale disturbances (natural and human-induced), could help to understand the maintenance of tree species richness.

# Introduction

The Atlantic laurel-forest or laurisilva (sensu Rübel 1930) is a montane cloud-forest considered as a late-Tertiary relict of the former Tethys Sea vegetation (Axelrod 1975). Although it has been considered as a 'tropical montane cloud forest' (Stadtmüller 1987; Hamilton et al. 1995), its location and other environmental characteristics make this forest very particular. An important characteristic in this forest is the high rate of asexual regeneration of trees (primarily by suckers). This characteristic is not reported as common in reviews about montane cloud forest or temperate forests (Ovington 1983; Stadtmüller 1987; Hamilton et al. 1995). The present distribution of the laurel forest comprises the archipelagoes of Azores, Madeira and Canaries, and is composed of several (ca. 30) tree-species, a major part of them endemic to the Macaronesian biogeographical region (Santos 1990). The anthropogenic disturbances dating to the XVth century (Parsons 1981) decreased the laurelforest extension of Tenerife to not more than 10% of its potential distribution (Figure 1), relegating the forest to the most inaccessibles areas. These particular characteristics make comparisons of dynamic processes with other montane cloud forests that are not in the Macaronesian region difficult.

Due to the mild climate prevailing in the laurelforest region, the windward slope at mid-elevations (600–1500 m) of the Canaries (Höllermann 1981; Marzol et al. 1988; Fernández-Palacios 1992), intense natural disturbances such as hurricanes and land-slides leading to large-scale forest destruction are rare. Despite the oceanic origin of the Canaries, there has been no volcanic activity in the last million years in the Anaga and Teno massifs (Ancochea et al. 1990), where the laurel forest occurs on Tenerife, to account for large-scale forest destruction. Outbreaks of pests or diseases have been revealed as an important factor in the dynamics of some forests (i.e. Liu Quinghong & Hytteborn 1991; Núñez-Farfán & Dirzo 1991), but these factors have been unnoticed in the laurel forest of Tenerife. Demographic processes leading to massive tree deaths, such as stand-level forest die-backs, reported on other oceanic archipelagos such as Hawaii (Mueller-Dombois 1987) or the Galápagos (Lawesson 1988), have not been reported for the Canaries; however, short declines of laurel forest found on La Gomera may have this origin (Mueller-Dombois pers. comm.). Small-scale disturbances seem more likely in the laurel forest. Large scale human induced disturbances are not common due to the inaccessibility of the remaining laurel forest of Tenerife.

The laurel forest composition has been well described but poorly analyzed in its dynamic processes (very common situation of montane cloud forest, Hamilton et al. 1995). In order to contribute to the understanding of the laurel-forest dynamics and diversity, we analyzed three laurel-forest plots. These analyses included both regeneration and canopy tree composition. We assumed that under similar geographic, climatic and edaphic stand conditions, the plots compared should bear similar canopy compositions. Differences under this assumption could therefore be related to different disturbance histories.

## Methods

# Study area

'El Moquinal' laurel-forest site, on the Anaga massif (NE corner of Tenerife, 28°19' N, 16°34' W) (Figure 1), includes two adjacent basins located between 750 and 800 m altitude exposed to the prevailing NE trade winds. The parent rock is a 3.7 Myr old basalt (Ancochea et al. 1990), whilst the soils have been classified in the order Entisol, suborder Orthens (Fernández-Caldas et al. 1982). The annual precipitation of the zone averages 900 mm, a quantity that can be doubled by the effect of local fog drip (Kämmer 1974). The mean annual temperature is 15.1 °C with scarcely any annual or daily oscillations so that frost does not occur.

The canopy height of Anaga's laurel-forest varies between 10 and 20 m depending on slope. Maxi-

mal heights are found at the basin's floor decreasing progressively towards the basin's borders. Dominant trees include *Laurus azorica*, *Erica scoparia*, *Erica arborea*, *Ilex canariensis*, *Prunus lusitanica*, *Myrica faya* and *Viburnum tinus* (Ceballos & Ortuño 1974). The laurel forest of Tenerife contains a total of 19 tree species (Santos 1990). The forest biomass is approximately 28 000 g m<sup>-2</sup> and net primary production is ca. 850 g m<sup>-2</sup> y<sup>-1</sup> (Fernández-Palacios et al. 1992).

#### Analytical procedure

We selected a basin in 'El Moquinal' site (one of the best-conserved laurel forests of Tenerife). In this basin we randomly located three  $20 \times 20$  m plots (A, B and C) under similar environmental conditions (altitudes between 770 and 800 m, NE wind-exposure, slopes between 25 and 30° and the same bed-rock). This scale provided a good representation of the area. A small scale allow a better relation of the results with biological interations because the environmental gradient is shorter (Wiens 1989). Within each plot we measured the relative basal area for each species (individuals >1.30 m). In order to consider both generative and vegetative reproduction strategies, we counted separately the number of seedlings and saplings (individuals < 1.30 m) and of suckers and basal shoots (vegetative offshoots < 1.30 m) per plot and expressed them as percentages per species in each plot. Leaf area indexes were estimated with a 'licor-LAI 2000' analyzer at 10 random locations in each plot, as well as 5 more under open sky in a nearby track as control.

In order to determine the composition of the seed bank, three randomly located samples per plot, comprising 1 kg of the first 5 cm of soil, were set to germinate under greenhouse conditions. The soil samples were placed in 5 cm-deep and 40 cm-diameter circular plastic trays that were daily irrigated 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 removed.

Nutrient variability could explain the existence of different patterns of regeneration between different areas. We considered it important to test the similarity in soil characteristics and nutrient availabilities across the three plots to reveal a possible effect in the species distributions. We carried out several soil analyses, collecting 1 kg-soil samples at three randomly selected locations per plot by excavating at



Figure 1. Actual (bold) and potential (stripes) distribution of the laurel-forest on Tenerife. 'El Moquinal' laurel forest station is located in the Anaga massif (source: Ceballos & Ortuño 1974).

two depths, 0-10 cm and 10-20 cm. We sieved (>2 mm), air dried, and stored aerobically each sample at room temperature. We measured soil pH by glass electrode, and organic carbon by the Walkley & Black procedure (Jackson 1976). Total nitrogen was measured following Bremner's (1960) method, while the soil phosphorus fractions were analyzed following the sequential extraction procedure of Hedley et al. (1982). Only the most labile fractions [phosphorus made extractable with anion exchange resins (resin-P) and bicarbonate-extractable Pi (Bic-Pi)] were measured. Phosphate in the extracts was measured by the malachite green colorimetric method (Fernández et al. 1985), whereas nitrate was analyzed according to the 'Brucine method' (Baker & Smith 1969). We determined exchangeable cations (sodium, calcium, potassium and magnesium) in ammonium acetate 1N (pH7) extracts by flame spectrophotometry.

We analyzed the effects of site, depth and interactions on soil analytical properties by a two-way analysis of variance (ANOVA). One way analysis of variance was used to test for differences between the plot's measures of leaf area index. We correlated the proportions of species basal area between plots, as well as the proportions of saplings and suckers. We used the proportions instead values because we are more interested in the comparison among distributions values.

Six species were included in these correlations. We used Spearman's rank correlation coefficient for these analysis. Basic statistical methods follow Zar (1984) and were implemented using the SPSS statistical package (SPSS Inc. 1990).

## Nomenclature

For the denomination of the species included in our analysis we followed Hansen & Sunding (1985).

# Results

We found no significant differences among plots and depths for any of the selected physical and chemical soil properties studied (Table 1), thus supporting the assumption of edaphic similarity among the plots. Moreover, the plots lacked significant differences in their leaf area indexes. Basal areas of the plots oscillated between 38.99 and 46.87 m<sup>2</sup> ha<sup>-1</sup> (Table 2).

The correlation of species basal area proportions among plots revealed non-significant relationships.

Depth (cm)	Plot A		Plot B		Plot C			
	0-10	10-20	0-10	10-20	0-10	10-20		
>2mm (%)	19.33(5.82)	25.99(4.03)	28.37(4.10)	18.99(5.58)	34.16(1.70)	40.39(4.87)		
Fraction								
pН	5.7(0.1)	5.5(0.1)	5.9(0.0)	5.7(0.0)	5.5(0.1)	5.4(0.1)		
Org. C (%)	9.99(2.27)	6.97(1.15)	10.04(2.07)	7.92(3.36)	10.42(0.82)	8.93(0.43)		
Org. C / total N	14.07(0.54)	11.86(1.02)	13.76(1.63)	12.94(0.12)	16.85(3.10)	14.23(0.41)		
Resin-Pi	6.49(3.66)	6.71(4.13)	9.71(0.05)	10.90(2.06)	10.63(1.23)	7.89(2.98)		
$(\mu g/g)$								
Bic-Pi	38.24(12.64)	27.01(4.39)	41.27(14.33)	27.70(14.00)	25.51(4.61)	14.79(3.15)		
$(\mu g/g)$								
N-NO <sub>3</sub>	12.88(5.65)	11.73(4.80)	9.30(4.26)	9.67(9.11)	11.89(2.02)	7.35(1.58)		
$(\mu g g^{-1})$								
Ex. cations								
(meq/100 g):								
Na	1.52(0.16)	1.38(0.26)	0.89(0.14)	4.88(2.39)	1.13(0.17)	1.18(0.12)		
K	1.85(0.34)	1.35(0.36)	2.03(0.59)	1.00(0.29)	2.03(0.12)	1.29(0.23)		
Ca	3.11(1.10)	2.81(0.82)	2.76(0.36)	2.39(1.07)	4.81(0.15)	2.91(0.11)		
Mg	7.78(1.92)	5.66(2.95)	5.71(0.87)	1.75(0.48)	7.68(0.38)	5.02(0.59)		

*Table 1.* Selected chemical and physical soil properties of the analyzed plots. Mean values (standard error) of three samples per plot are given. Significant differences among plots and soil depths were not found for any measured parameters.

We could assume that the plots have significant differences in the proportions of species basal area. In plot B *Myrica faya* and *Erica arborea* were the dominant (with respect to the analyzed parameter) species while in plot A and C the dominant species were *Prunus lusitanica*, *Laurus azorica* and *Ilex canariensis* (in plot C we have included also *M. faya*) (Figure 2a).

The regeneration composition (seedlings and suckers) and the seed bank follow the same pattern in the three plots (Figures 2b, 2c and 2d). *Laurus azorica* is the dominant seedling species in all of the plots, independent of their canopy composition. *Viburnum tinus*, very scarce in the canopies of all three stands, is the second most abundant seedling in all the plots. The remainder of the species have very few (*Prunus lusitanica, Picconia excelsa, Myrica faya* and *Ilex canariensis*) or even no (*Erica arborea*) seedlings (Figure 2b). *P. lusitanica* is the dominant sucker in all plots, independent of their canopy composition. *I. canariensis* and *L. azorica* show vegetative reproduction to a lesser degree, whereas suckering is almost nonexistent in the remainder of the species (Figure 2c).

Almost an absolute dominance of *Erica arborea* in the germinated species of the seed bank was revealed, providing together with the fern *Asplenium onopteris* more than 95% of all germinated diaspores. On the other hand, *Myrica faya*, *Laurus azorica* and *Ilex per*- *ado*, as well as some herbs, are barely represented in the seed bank of 'El Moquinal' forest. The rest of the tree-species are either absent, or their seeds have not yet germinated after two years under greenhouse conditions (Table 3, Figure 2d). We found a small variability in the seed-bank germination of the different trays.

# Discussion

We found that regeneration and seed bank composition are not significantly different between plots. These results are remarkable in light of the marked differences in the composition of basal area of trees (>1.3 m).

Regarding seedling regeneration, the absence of *Myrica faya* and *Erica arborea* seedlings under the current environmental conditions is noticiable (Figure 2b), despite their existence as viable seeds in the seed bank (these results follow the same patterns of others seed-banks studies conducted in the area). This suggests that these species have been recruited under different environmental conditions. The environmental sieve (Harper 1977; Keddy 1992) was very likely characterized by intense light conditions, as a consequence of a previous natural or man-induced disturbance that led to the creation of a forest-gap.

	Plot A					Plot B <sup>(*)</sup>					Plot C					
Species	Pl	Ic	La	Ea	Vt	Pl	Ic	La	Ea	Vt	Mf	Pl	Ic	La	Vt	Mf
No. trees $(h > 1.30 \text{ m})$	103	61	30	1	2	22	37	18	29	_	10	44	27	27	2	2
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	27.22	10.1 0	7.45	2.06	0.03	4.66	6.38	3.47	11.70	-	14.98	17.65	5.55	8.72	0.02	7.06
No. seedlings	6	-	57	_	15	14	5	437	-	19	-	1	-	146	45	1
No. suckers	438	10	44	_	4	132	12	58	_	-	1	109	19	16	-	1
Regeneration Patterns																
% seedlings	1.4	0	56.4	_	78.9	9.6	29.4	88.3	_	100	(+)	0.9	0	90.1	100	(+)
% suckers	98.6	100	43.6	-	21.1	90.4	70.6	11.7	-	0		99.1	100	9.9	0	
Plot basal area	46.87					43.15						38.99				
L.A.I. <sup>(**)</sup>	4.80 (0.15)				5.49 (0.07)					5.13 (0.09)						

Table 2. Number of trees, basal area of adults, number of seedlings and suckers per plot (400 m<sup>2</sup>) and leaf area indexes of the plots analyzed.

Species code: (*Pl*) *Prunus lusitanica*, (*Ic*) *Ilex canariensis*, (*La*) *Laurus azorica*, (*Ea*) *Erica arborea*, (*Vt*) *Viburnum tinus*, and (*Mf*) *Myrica faya*. (+) Too few items.

(\*) Picconia excelsa (Pe) and Ilex perado (Ip), appearing only in plot B with a basal area < 5% were left out from further studies.

(\*\*) Mean LAI values and standard error, in brackets, are given. Significant differences were not found.

Species	Seed bank samples									
	A1	A2	A3	B1	B2	B3	C1	C2	C3	sp. total
Trees										
Erica arborea	48	36	75	458	128	101	19	19	174	1058
Myrica faya						1			19	20
Laurus azorica						7				7
Ilex perado		1								1
Herbs										
Hypericum inodorum		3	2					4		9
Ixanthus viscosus				1			1			2
Juncus sp.				1					1	2
Cedronella canariensis			1							1
Ferns										
Asplenium onopteris	14	9	4	197	12	13	14	64	71	398
Dryopteris oligodonta									1	1
Sample total	62	49	82	657	140	122	34	87	266	1499

Table 3. Number of propagules germinated under greenhouse conditions (November 94-November 96)



*Figure 2*. Percentage of the plots's (a) basal area, (b) number of seedlings, (c) number of suckers and (d) number of germinated seeds accounted by each species. Below each graph are indicated the Spearman correlation coefficients among plot combinations (n = 6) of basal area proportions (below graph 'a'), seedlings proportions (below graph 'b') and suckers proportions (below graph 'c'). Significant levels are: (\*): p < 0.05; (\*\*): p < 0.01; ns: non significant. Species with this regeneration ecology are considered 'pioneer' (Whitmore 1989). These species produce many small, easily-dispersed seeds that remain viable in the seed bank for a long time. Nevertheless, these seeds can not germinate under the shade of closed forest canopies, and thus pioneer species are not able to perpetuate due to the shade produced by their own adult individuals. Canopy gaps are well known to increase light levels and nutrient availability sufficiently to influence the dynamics of the tree regeneration (Denslow 1987). Some tree species have developed such specific physiological mechanisms (Oliver & Larson 1990), that they show regeneration cycles synchronized with the disturbance regime (Johnson 1981; Runkle 1982, 1984).

For the Canarian laurel-forest, the presence of *Myrica faya* has even a wider effect for the community, due to its role as unique nitrogen-fixing species of this forest. This effect of *M. faya* has been clearly shown on the island of Hawaii, where after its introduction the N income of the native forest ecosystems is increasing, fixing as much as 18 kg ha<sup>-1</sup> yr<sup>-1</sup> (Vitousek & Walker 1989). It is now considered one of the worst pests on the islands (Vitousek et al. 1989).

Furthermore, both *Erica arborea* and *Myrica faya* are the co-dominant species of a laurel-forest related vegetation type: the 'fayal-brezal', a 5–10 m tall woody-heath. This heath has a spatial distribution closely related to the laurel-forest: wind-prone mountain crests of the windward slopes, and transition zones to the pine forest at 1300–1500 m a.s.l, where it is considered potential natural vegetation (Santos 1990).

*Laurus azorica* and to a lesser extent *Viburnum tinus*, show a regeneration pattern characterized by a high number of seedlings growing under closed canopies. These species could be classified as 'non-pioneer' or 'shade tolerant' (Brokaw & Scheiner 1989; Whitmore 1989) and produce relatively few, large and poorly dispersed seeds which can germinate in the shade due to their accumulated reserves. Seedlings of such species can establish and eventually grow to maturity (as seems to be the case for *V. tinus*) in the shade. A tree-fall often permits a small, single-cohort stand to grow from 'advance regeneration' (Bormann & Likens 1979).

Neither *Prunus lusitanica* nor *Ilex canariensis* seemed to follow any of the two strategies described above. Although these species bear established seedlings under the closed canopy, and thus fit the climax concept, they showed a different reproductive

strategy (more than 70% of total regeneration in these species is asexual in the three plots) compared to *Laurus azorica* and *Viburnum tinus* (less than 45%) (cf., Table 2; Figures 2b and 2c). Due to the importance of vegetative reproduction in these species, their growthform consists of more multi-stem individuals than of single-stem individuals. These trees could be defined as 'remnant species' (Erikson 1996) and are characterized by their high percentage of vegetative offspring compared to the number of seedlings.

Vegetative shoot survival rates, due to the high investment of resources involved, have been found to be much higher than survival rates for seedlings (Fenner 1985). Conversely, both pioneer and conventional climax species invest less energy in spatial persistence than in seed production, which increases the probability of reaching suitable sites (Hubbell & Foster 1986). A high rate of asexual regeneration has been related to mid-successional communities (Bazzaz 1996) and a low disturbance level (Packham et al. 1992).

Despite the similarity of sexual and asexual reproduction strategies among plots, the replacement processes of the canopy will vary due to the actual differences found in the canopy compositions. The combination of sexual and asexual regeneration appears to maintain species composition in plot A and C. Without major disturbances, we do not expect major changes through time. In contrast, the vegetation in plot B (now dominated by Myrica faya and Erica arborea), appears to be proceeding towards a forest dominated by Prunus lusitanica, Laurus azorica and *M. fava*, such as can be found today in plot C. Later, regeneration is likely to result in forest dominated only by P.lusitanica and L.azorica. However, pioneer species could persist longer during succession. By persisting for longer periods of time it is more likely that a disturbance will occur which will favor these pioneers. Also, this could allow the occupation of new areas. A long persistence in the seed-bank (more than 2 years) of these species and the continuous renovation of the bank from individuals of the forest border, will contribute to the maintenance of these species.

The results of our study support the existence of these three regeneration strategies. Regeneration composition proved to be similar in the three sites considered. The maintenance of similar regeneration composition under different canopy composition has been related to late successional states (Horn 1975). We suggest the remaining laurel forest of Tenerife to be in a mid-late successional state. We believe that the present approach pointed to stand history (directly related with natural or human induced disturbances) as an important factor to understand the current floristic tree composition of the laurel-forest. We conclude that the laurel-forest diversity could be attributed to the existence of at least three different ecological groups of trees, pioneer, climax and remnant species, together with the spatial and temporal unpredictability of short-scale disturbance events leading to tree-falls.

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