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Treefall gap characteristics and regeneration in the laurel forest of Tenerife

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Abstract. We conducted a study in the laurel forest of Tenerife (Canary Islands, Spain) to describe the characteristics of natural gaps and to assess the role of treefall gaps in forest dynamics. Very little is left of the natural laurel forest with *i.a. Laurus azorica*, *Ilex canariensis* and *Prunus lusitanica*. We looked for treefall gaps in 80 randomly located 2500 m^2 plots. These plots represented ca. 1 % of the remaining and protected laurel forest of Tenerife. We recorded the characteristics of the species causing the gaps, gap architecture and gap age in all observed gaps larger than 10 m^2. We inventoried the regeneration in each gap and in a neighbouring control plot with the same topography. Large gaps (> 75 m^2) were not common in the laurel forest. The absence of large gaps could be due to the physiognomy of the vegetation, the mild weather or the rarity of disturbances. Instead of forming gaps, many trees decompose in place and branches from neighbouring trees and suckers from the decomposed trees occupy the free space. Also, the high rate of asexual regeneration could contribute to the fast closing of the gap.

The number of gaps created by *Prunus lusitanica* was higher than expected (based on canopy composition) while *Ilex canariensis* and *Laurus azorica* created fewer gaps. In this evergreen forest, differences between gap and non-gap conditions are not as distinct as in other forest types. Only 0.4 % of the canopy is in the gap phase (0.6 % including gaps smaller than 10 m^2). No differences were found in patterns of regeneration between gap and non-gap phases in the forest. Gaps do not explain the persistence of pioneer species in the laurel forest.

Keywords: Forest dynamics; Gap theory; Gap-maker; Sapling; Seedling; Sucker.

Nomenclature: Hansen & Sunding 1985.

Introduction

Treefall disturbance affects ecological processes in forests (Platt & Strong 1989; Denslow & Spies 1990), producing the cyclic phenomenon known as gap dynamics (*sensu* van der Maarel 1988, 1996). The frequency of gap formation plays an important role in species regeneration (Hartshorn 1980) and determines many structural aspects of the forest (Runkle 1991). The influence of canopy openings on sapling growth, survival, and the probability of a tree attaining canopy status has been tested in several studies (Martínez-Ramos 1985; Hubbell & Foster 1986; Runkle 1990; Westman 1990; Cho & Boerner 1991; Poorter et al. 1994; Denslow 1995; Lusk 1996; Gray & Spies 1996). Spatial patterning of canopy gaps has also been reported (Poorter et al. 1994; Battles et al. 1995). Although the study of forest gaps has been useful for understanding the dynamics of many forests, some authors note that there are few generalizations about the role of forest gaps (Denslow 1987; Kapos et al. 1990). In some forests, the gap/non-gap paradigm is not useful for explaining replacement of species (Midgley et al. 1995; Lieberman et al. 1989).

We conducted the present study in the laurel forest of Tenerife, Canary Islands. Rugged topography enables only limited exploitation of the forest, which is therefore well preserved. We have no information about the age of the forest but we believe that this evergreen forest is (at least) several generations of trees old.

The dynamics of this forest are largely unknown, and in addition to more traditional works about forest composition and structure (Anon. 1973), only a few quantitative vegetation studies have been published (Fernández-Palacios 1992; Fernández-Palacios & de Nicolás 1995). Today, only 10 % of the original laurel forest of Tenerife remains (Santos 1990). The purpose of the present study was to determine treefall gap characteristics, their effect on regeneration and to discuss the implications of these results for gap theory.

Material and Methods

Study area

The study sites were located in the Anaga Natural Park (NE part of Tenerife; 28°19' N, 16° 34' W), an area encompassing a 7 - 8 million yr old basaltic massif of 150 km^2 (Ancochea et al. 1990). We sampled four sites comprising the best remnants of laurel forest in the Park: El Moquinal, Vueltas de Taganana and El Pijaral on the windward slope and Monte de Aguirre on the leeward slope. Our 2000-ha study area comprises all of the extant laurel forest of Tenerife except for a small remnant in the western part of the island.

Annual precipitation in the park amounts to 900 mm, but would be twice this amount if fog drip from the trade winds is included (Kämmer 1974). Mean annual temperature is close to 15.0 °C with small annual and daily fluctuations. There are no frost events. Soils of the study have been classified in the order Entisol, suborder Orthens (Fernández-Caldas et al. 1985).

The canopy height of Anaga's laurel-forest varies with slope position. Mean heights decrease progressively from basin floors (20 m) to upper slopes (10 m). Dominant trees include *Laurus azorica*, *Erica scoparia*, *Erica arborea*, *Ilex canariensis*, *Prunus lusitanica*, *Myrica faya* and *Viburnum tinus* (Anon. 1973). The forest understorey is composed of seedlings and saplings of those species in addition to some herbs and ferns. Further information about the study site is given in Fernández-Palacios et al. (1992).

Data collection

From September 1995 to February 1996, we established 80 square plots each of 2500 m^2. We randomly located 20 plots in each of the four sites and checked the canopy for gaps. All gaps with more than half of their projection inside the plot were considered to be in the plot. We did not use the transect method of sampling (Brokaw 1985) because we could not establish a long line without intersecting roads, precipices, or other obstacles.

We used two definitions of gaps:

Gap projection: We used van der Meer & Bongers (1996) modification of Brokaw's (1982) definition of gap, that determines the size of the opening at 20 m height. However, we used a vegetation height of 10 m, which is more appropriate to the stature (ca. 10 m) of this forest.

Expanded gap: The area circumscribed by the stem bases of all trees that border the gap (Runkle 1981).

The differences are important, because under the second definition gaps include the area directly and indirectly affected by the canopy openings. We were interested in how patterns of regeneration could be affected by this opening. We also analysed the gap transition (the area of expanded gap not in the area of gap projection).

The area of gaps larger than 10 m^2 was estimated from a scale map drawn using the distances from the center of each gap to the perimeter along eight compass headings (0, 45, 90, 135, 180, 225, 270 and 315 °). We calculated the area of the expanded gap in a similar manner using the area defined by a polygon constructed using the trees whose crowns border the canopy opening (Runkle 1992). Although Green (1996) remarked that this method could underestimate areas by 10 - 20 %, we used it so that comparisons could be made with forests described using similar methods.

In gaps larger than 10 m^2 we determined the species of gap-maker, tree height, tree diameter at breast height (DBH) and direction of fall. We also noted whether the gap-maker was uprooted or alive. Slope, orientation, UTM (Universal Transverse Mercator grid) coordinates and altitude of each gap were recorded. In each gap projection, expanded gap and transition, all seedlings, saplings and suckers were counted. Seedlings were identified as individuals less than 15 cm tall because the majority of tree species less than one year old do not exceed 15 cm. Saplings were defined as being greater than 15 cm in height and less than 5 cm DBH. Suckers were the products of asexual reproduction, having the same point of origin as the parent tree and a size greater than 15 cm tall and less than 5 cm DBH. All trees with stems > 5 cm DBH were taken into consideration.

A 100 m^2 control plot was established ca. 10 m from the border of each gap projection. This distance is presumed to be sufficient to avoid the influence of an open canopy given the low stature of the vegetation. The control plot was established in an area topographically and orographically similar to the gap. We measured the basal area of the trees in the plot. We also counted the number of seedlings, saplings and suckers in a 25 m^2 subplot located in a randomly chosen corner.

We estimated the area of gaps smaller than 10 m^2 – 3 m^2 was the smallest gap we could determine – using the formula $A = \pi LS / 4$ (Runkle 1981; Cho & Boerner 1991) in which L is the longer diameter and S is the shorter. The area in these gaps was measured to estimate their contribution to the total canopy opening of the forest.

Data analysis

The expected numbers and basal areas of the gap-makers were calculated from the percentages of densities and basal areas from the control plot: The species percentages (using basal area) of each control plot were normalized with the values of total number and basal area of the gap-makers to obtain the expected number and basal area of the gap-makers per species. These expected values were compared with the observed values using the nonparametric Wilcoxon Rank Sum W test. The sample size varied because some species were not always present in both the control plots and gaps. We excluded from the analysis species which were present in less than seven gap-control plots.

The relationships between gap size (using the two definitions) and the numbers of gap-makers, total basal area of gap-makers, slope and vegetation height were investigated using the Spearman rank correlation coefficient.

The differences among species densities in control and gap projection and among control and gap transition areas for seedlings, suckers and saplings were tested by a randomization *t*-test (non-normal errors and many ties made this test suitable) using 500 iterations (Edgington 1985). The gap projection composition was ordinated with Canonical Correspondence Analysis (CCA) and a Redundancy Analysis (RDA) to reveal a possible gradient of species composition related to gap size, considered the explanatory variable on the analysis. We separately analysed the seedlings, saplings and suckers composition to investigate the relationship between species composition and gap status (gap projection, gap expanded and control areas). We used the CANOCO package (ter Braak 1988) for these analyses – we checked our results in view of the problems described by Podani (1997) and Oksanen & Minchin (1997), and found them to be correct.

Statistical methods (Zar 1984) were implemented using the SPSS statistical package (Anon. 1990).

Table 1. Gap characteristics in the laurel forest of Anaga. Only gaps larger than 10 m^2 were considered. (std = standard deviations; veg h = vegetation height in m; area in m^2; slope in °.

Number of gaps on 20 ha	21
Mean slope (std)	31.2 (2.2)
Mean veg h (std)	12.0 (2.8)
Mean gap-makers/gap (std)	5.7 (3.7)
Percentage single gaps (1 gap-maker)	4.8
Percentage gaps < 1 yr old	4.8
Percentage gap-makers alive	78.5
Percentage gap-makers uprooted	85.0
⁺Gap projection. Mean area/gap (std)	40.65 (25.31)
⁺Expanded gap. Mean area/gap (std)	77.65 (37.22)
% canopy in gap projection	0.42
% canopy in expanded gap	0.81
* % canopy opened for gaps < 10m^2	0.22

* For gaps < 10 m^2 only gap projection was measured.
\+ Only gaps larger than 10 m^2 included.

Results

We found 21 gaps larger than 10 m^2 in the 80 plots of 2500 m^2 and the estimated percentage of total canopy in the gap phase was 0.4 % for the gap projection definition, and 0.6 % when the area of gaps smaller than 10 m^2 is included. Using the expanded gap definition, 0.8 % of the canopy is in the gap phase. Only one of the gaps was produced in the year before sampling and only one of the gaps was produced by a single gap-maker (Table 1). The range of variation of gap projection size was between 17 and 125 m^2. We obtained a mean gap size of 40.6 m^2 and 77.6 m^2 based on gap projection and expanded gap definitions (for gaps > 10 m^2). Gaps smaller than 10 m^2 were very common, representing 34 % of the total open canopy and and more of 80 % of the total number of gaps. The most important gap size class for gaps > 10 m^2 was between 20 and 30 m^2, with seven gaps. This size class also had the largest percentage area of total open canopy (Fig. 1).

13 tree species occurred in the control plots. *Laurus azorica*, *Prunus lusitanica* and *Ilex canariensis* (shade-tolerant species) showed the greatest density and basal area of any species in the control plots (Table 2). *L. azorica*, *Viburnum tinus* and *P. lusitanica* all had high values for the regeneration classes. These three species

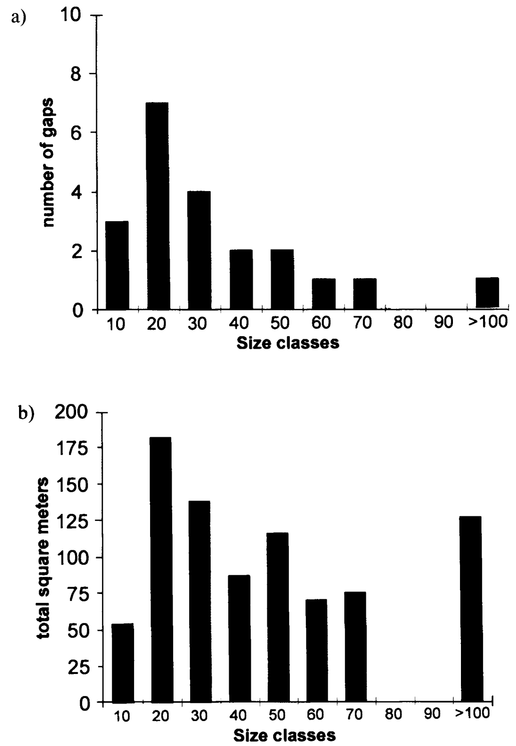

Fig. 1. Size distribution of **a.** number of gaps ($n = 21$) and **b.** total area of gaps on 20 ha. Size classes: 10 = 10 - 20 m^2, 20 = 20 - 30 m^2, etc.

Table 2. Mean density and basal area of trees in 21 control plots of 100 m^2. Mean densities of regeneration in 20 plots of 25 m^2 for seedlings, suckers and saplings and total regeneration (in one of the gaps it was not possible to measure the regeneration; only the basal areas of the trees was measured). Standard deviations are in parentheses.

		Basal area	Regeneration (stems/100m^2)			
Species	Trees/ha	(m^2/ha)	Seedlings	Saplings	Suckers	Total
Apollonias barbujana	4.76 (21.79)	0.01 (0.06)	0.30 (1.10)	0.80 (2.60)	-	0.98 (3.47)
Erica arborea	276.19 (530.00)	3.51 (7.08)	-	-	0.40 (1.20)	0.40 (1.20)
Erica scoparia	428.57 (835.76)	5.44 (10.15)	-	-	-	-
Heberdenia excelsa	47.62 (107.24)	0.09 (0.27)	0.90 (3.60)	1.10 (2.50)	-	1.85 (5.31)
Ilex canariensis	514.29 (512.25)	4.70 (4.48)	-	0.10 (0.20)	1.20 (5.10)	1.25 (5.22)
Ilex platyphylla	185.71 (390.48)	5.29 (10.71)	-	0.20 (0.90)	3.20 (9.40)	3.40 (9.57)
Laurus azorica	1080.95 (630.36)	15.08 (9.53)	7.10 (9.10)	6.80 (8.80)	11.10 (14.00)	24.5 (20.28)
Myrica faya	195.24 (362.59)	3.24 (5.36)	-	-	0.90 (2.70)	0.90 (2.70)
Ocotea foetens	95.24 (270.19)	1.61 (4.39)	-	-	0.20 (0.90)	0.20 (0.90)
Persea indica	9.52 (43.59)	0.61 (2.78)	0.20 (0.70)	0.10 (0.20)	0.20 (0.90)	0.41 (1.17)
Picconia excelsa	47.62 (177.48)	0.16 (0.68)	0.20 (0.70)	1.30 (3.90)	0.20 (0.90)	1.55 (3.81)
Prunus lusitanica	519.05 (700.34)	8.86 (17.75)	-	1.70 (4.60)	4.80 (10.00)	6.20 (11.89)
Rhamnus glandulosa	-	-	0.30 (1.10)	0.30 (0.90)	-	0.53 (2.79)
Viburnum tinus	63.42 (121.35)	0.65 (0.96)	3.20 (4.20)	8.30 (7.90)	2.80 (3.40)	12.95 (11.78)
Total	3505.50 (1143.01)	50.57 (19.49)	11.42 (14.72)	19.66 (18.97)	24.19 (20.07)	55.95 (36.09)

comprised more than 75 % of the total regeneration of the control plots. All trees species were represented in the smaller size classes except one (*Erica scoparia*). All species found in the smaller size classes were also found in the tree stratum except one, *Rhamnus glandulosa*. No seedlings were found for seven species in the control plots, but three of these were present as saplings in the control plots. Of the other four species, three occurred as suckers and only *E. scoparia* was absent from all regeneration types. All but four of the 13 canopy species were found as suckers in the control plots and three of these four were found as suckers in the gap plots (Table 2). We only have data for 20 control plots for regeneration (vs. 21 gaps) because in one of the gaps it was not possible to measure the regeneration due to the near vertical topography. However, we did measure gapmakers in this gap, and also inventoried the trees of its control plot.

The mean density of regeneration in the different gap areas is shown in Table 3 for seedlings, saplings and suckers. Regeneration size classes and types for all fourteen canopy species were found in some part of the gaps. *L. azorica*, *Viburnum tinus* and *P. lusitanica* had the highest densities of regeneration. Densities were highest in the gap transition area (100.2 stems/100 m^2 but were nearly identical in the control plots (56.0 stems/100 m^2) and gap projection areas (53.4 stems/100 m^2). *Erica arborea*, *Myrica faya* and *Ocotea foetens* had sexual regeneration (seedlings and saplings) in at least one of the areas of the gaps, but they did not show sexual regeneration in the control plots. Dominant species of the canopy, *L. azorica*, *P. lusitanica* and *V. tinus* were

Table 3. Mean density of regeneration in gap projection, expanded gap and gap transition areas for seedlings, saplings and suckers. Standard deviations are in parentheses. n = 20.

	Regeneration (stems/100m^2)								
	Gap projection			Expanded gap			Gap transition		
Species	Seedlings	Saplings	Suckers	Seedlings	Saplings	Suckers	Seedlings	Saplings	Suckers
Apollonias barbujana	1.33 (5.96)	2.43 (6.83)	0.80 (3.57)	1.01 (4.01)	2.81 (6.48)	1.11 (4.01)	0.24 (1.06)	2.92 (7.93)	1.55 (4.80)
Erica arborea	-	0.69 (1.45)	0.12 (0.56)	0.04 (0.18)	0.67 (1.68)	0.30 (1.11)	0.11 (0.50)	0.73 (3.19)	0.67 (2.08)
Erica scoparia	-	-	0.12 (0.56)	-	-	0.08 (0.35)	-	-	-
Heberdenia excelsa	-	1.11 (3.89)	0.42 (1.87)	-	1.74 (6.01)	0.13 (0.55)	-	2.41 (8.90)	-
Ilex canariensis	-	0.76 (1.88)	1.40 (3.33)	-	0.32 (0.77)	2.16 (4.78)	-	0.32 (1.10)	2.75 (6.47)
Ilex platyphylla	0.17 (0.75)	0.21 (0.93)	0.21 (0.93)	0.26 (0.98)	0.31 (1.03)	0.10 (0.34)	0.37 (1.36)	0.22 (0.98)	0.13 (0.55)
Laurus azorica	4.61 (7.71)	9.36 (17.10)	4.48 (10.45)	7.36 (10.62)	10.78 (17.23)	8.34 (14.02)	10.34 (20.33)	12.02 (18.00)	13.69 (22.96)
Myrica faya	-	0.36 (1.62)	0.28 (1.24)	-	0.21 (0.73)	0.36 (1.58)	-	0.21 (0.73)	0.39 (1.72)
Ocotea foetens	-	0.19 (0.83)	-	0.08 (0.37)	0.22 (0.54)	-	0.16 (0.69)	0.27 (0.83	-
Persea indica	0.80 (3.57)	0.21 (0.94)	0.28 (1.24)	0.55 (2.41)	0.25 (1.09)	0.37 (1.10)	-	0.29 (1.27)	0.54 (2.35)
Picconia excelsa	-	-	-	-	0.59 (1.75)	-	-	1.64 (5.03)	-
Prunus lusitanica	-	0.71 (1.80)	5.31 (11.20)	0.13 (0.55)	0.86 (1.22)	5.93 (7.78)	0.29 (1.27)	1.06 (2.47)	7.98 (16.87)
Rhamnus glandulosa	0.27 (1.19)	0.21 (0.94)	-	1.05 (4.02)	0.13 (0.55)	-	2.44 (9.41)	-	-
Viburnum tinus	3.95 (8.71)	6.01 (7.36)	4.30 (12.04)	5.15 (13.04)	8.81 (10.78)	9.61 (20.49)	6.59 (20.97)	12.84 (18.90)	17.13 (37.50)
Total	11.67 (21.02)	23.35 (30.79)	18.41 (23.94)	15.01 (30.61)	27.70 (34.66)	28.52 (38.62)	20.57 (44.09)	34.79 (45.13)	44.82 (76.42)

Table 4. Mean density of total regeneration (seedlings, saplings and suckers) in gap projection, expanded gaps and gap transition areas.

	Total regeneration (stems/100m^2)		
Species	Gap projection	Expanded gap	Gap transition
Apollonias barbujana	4.56 (15.69)	4.90 (12.76)	4.48 (10.36)
Erica arborea	0.86 (1.52)	1.04 (2.21)	1.51 (4.53)
Erica scoparia	0.12 (0.56)	0.08 (0.35)	-
Heberdenia excelsa	1.38 (4.89)	1.86 (6.54)	2.41 (8.90)
Ilex canariensis	1.97 (4.09)	2.47 (4.99)	3.06 (6.43)
Ilex platyphylla	0.90 (2.29)	0.67 (1.58)	0.72 (1.67)
Laurus azorica	19.32 (29.97)	26.60 (36.98)	36.04 (52.24)
Myrica faya	0.67 (2.08)	0.57 (1.73)	0.47 (1.77)
Ocotea foetens	0.19 (0.83)	0.30 (0.82)	0.43 (1.44)
Persea indica	1.34 (3.86)	1.16 (3.37)	0.83 (2.61)
Picconia excelsa	-	0.59 (1.75)	1.64 (5.03)
Prunus lusitanica	6.31 (11.56)	6.91 (8.38)	9.32 (17.22)
Rhamnus glandulosa	0.49 (1.51)	1.17 (4.10)	2.44 (9.41)
Viburnum tinus	15.00 (25.47)	23.31 (41.33)	36.56 (73.69)
Total	53.44 (66.81)	71.24 (94.23)	100.18 (155.80)

also dominant in the regeneration in all regeneration classes and areas.

Suckers were the most important way of reproduction in both control and gap transition plots; suckers ranked second only in gap projection areas (saplings were first in these plots). Only one species in the regeneration in gaps was not observed in the canopy: *Rhamnus glandulosa* – which was never observed as a sucker (Tables 2 and 4).

Laurus azorica was the most common tree (ca. 33 % of tree stems) and the leading species in regeneration size classes in both control and gap plots. This species was ranked number one for all sizes and types of regeneration except for saplings in control plots (it was second to *Viburnum tinus*) and suckers in the gap projection plots (it was second to *Prunus lusitanica*). *P. lusitanica* was the second most common tree (ca. 17 % of tree stems) and it was well-represented in all situations except that it lacked seedlings in control and gap projection plots. *Ilex canariensis* was the third most common tree (also ca. 17 % of the tree stems) and it was present in most size classes and microsites, but it had a lower relative density in the regeneration compared to the canopy trees. *Erica scoparia* was the fourth most common tree (ca. 11 % of the stems) but was very much underrepresented in the regeneration size classes and microsites, being present only as suckers in the gap projection and expanded gap samples. *Erica arborea* was the fifth tree (ca. 9 % of the stems) but it was also generally underrepresented in the regeneration samples.

By contrast, several species were much more important in the regeneration than in the tree stratum. These include *Viburnum tinus*, which was the second leading regeneration species in the control samples and either the first or second leading species in the three kinds of gap samples. This species was only the 10th species (1.5 % of tree stems) but it included ca. 30 % of all regeneration stems. Other species which were more important in regeneration than in the canopy were *Apollonias barbujana* and *Rhamnus glandulosa* (Tables 2 to 4).

The most common gap-makers were dominant canopy species. *Prunus lusitanica*, *Laurus azorica* and *Viburnum tinus* made up the majority of the total gap-makers (60 %, 9 % and 7 % respectively). The majority of gap-makers also had live stems, but we did not find living gap-makers of the shade-intolerant species *Erica scoparia*, *Erica arborea* and *Myrica faya* (Table 5).

The mean number and basal area of gap-makers per gap were compared with the expected values. The observed mean number of gap-makers per gap of *Prunus lusitanica* was significantly higher than expected while for *Laurus azorica* and *Ilex canariensis* it was lower ($p < 0.01$). When we compared observed basal area with

Table 5. Summary of gap-maker characteristics in the 21 gaps found in the four stations sampled. Standard deviations in parentheses.

Species	No. gap-makers	% live	% uprooted	DBH (cm) mean (std)	Height (m) mean (std)
Erica arborea	6	0	83.3	20.58 (10.41)	7.17 (2.50)
Erica scoparia	6	0	100	13.05 (4.01)	7.75 (1.71)
Ilex canariensis	3	100	33.3	11.78 (3.00)	7.00 (0.50)
Ilex platyphylla	5	100	100	13.56 (3.45)	9.84 (0.60)
Laurus azorica	11	72.7	36.36	18.27 (9.92)	3.22 (9.90)
Myrica faya	4	0	75	18.50 (5.97)	9.93 (1.89)
Persea indica	1	100	0	11.14	(*)
Picconia excelsa	1	100	0	7	5.4
Prunus lusitanica	73	97.2	78.1	14.91 (6.88)	8.70 (3.08)
Rhamnus glandulosa	2	100	0	12.89 (7.16)	10.50 (2.50)
Viburnum tinus	9	100	44.4	6.51 (2.38)	5.68 (0.93)

(*) The decomposition of the trunk made it impossible to determine its height.

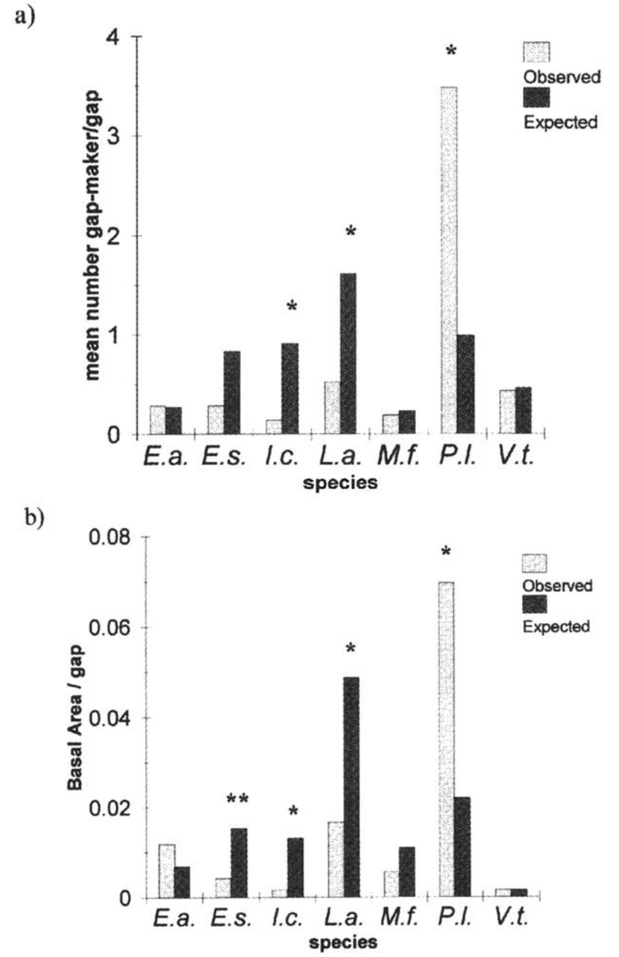

Fig. 2. a. Mean number of gap-makers and **b.** mean basal area in m^2/ha of gap-maker expected and observed per gap. Significant differences between expected and observed (Wilcoxon test): ** $P < 0.05$ and * $P < 0.01$). For other species sufficient data are not available. E.a. = *Erica arborea*, $n = 8$; E.s. = *Erica scoparia*, $n = 8$; I.c. = *Ilex canariensis*, $n = 15$; L.a. = *Laurus azorica*, $n = 20$; M.f. = *Myrica faya*, $n = 8$; P.l. = *Prunus lusitanica*, $n = 17$; V.t. = *Viburnum tinus*, $n = 14$.

expected, the observed mean basal area per gap of *P. lusitanica* was higher than expected while for *L. azorica*, *I. canariensis* and *Erica scoparia* it was lower ($p < 0.01$ except for *E. scoparia* which $p < 0.05$). Observed values for the rest of the species were not different from the expected values (Fig. 2). Gap size (gap projection and expanded gap) was positively correlated with the number of gap-makers and the total basal area of gap makers, but the correlation was strongest for expanded gaps. No relationships were found between gap size and slope or vegetation height, therefore our study did not reveal effects of a site quality gradient within the sampling area (Table 6).

Table 6. Spearman correlation coefficients between the number of trees (No. ind.) and basal area (Total b.a.) of fallen trees, slope and vegetation height (Height veg.) and the size of the gap following the two methods. All gaps were considered ($n = 21$).

Gap size method	No. ind.	Tot. b.a.	Slope	Height veg.
Gap projection	0.37^{**}	0.42^{**}	0.07^{ns}	0.22^{ns}
Expanded gap	0.51^{*}	0.48^{**}	0.13^{ns}	0.27^{ns}

**$p \leq 0.05$; *$p \leq 0.01$; ns: not significant.

Canonical Correspondence Analysis revealed that the variability of species composition of the 20 gap projection areas cannot be explained by the size of the gap for any of the three regenerative classes: seedlings, saplings and suckers. The first eigenvalues of these three analyses were 0.018, 0.067 and 0.052, respectively and the Monte Carlo test for axis 1 was not significant in any of the three analyses. Also, the explanatory variables gap projection, expanded gap and control areas did not explain the variance in species composition for the regeneration classes seedling, sapling and sucker. The eigenvalues of axes 1 and 2 for the analysis of the seedlings were 0.113 and 0.025, for the analysis of the saplings 0.060 and 0.008 and for the analysis of the suckers 0.124 and 0.005. The cumulative percentage of variance of species data for both axes in the three analysis was less than 3.5 %. The Monte Carlo test for axis 1 was not significant in the three analysis. Redundancy Analysis produced results similar to that of CCA.

The randomization *t*-test between regeneration densities of control plot and gap projection showed significantly ($p < 0.01$) smaller densities of seedlings and suckers of *Laurus azorica* and seedlings and saplings of *Viburnum tinus* in the gap projection. Saplings of *L. azorica* had significantly higher densities in the gap projection. The test between control plot and gap transition showed significantly ($p < 0.01$) higher densities of seedlings, saplings and suckers of *L. azorica* and saplings and suckers of *V. tinus* in the gap transition.

Discussion

A low percentage of the canopy of this forest is in the gap phase. The percentage of forest in the gap phase is summarized as 5 - 31 % for temperate and 1.4 - 23 % for tropical forests (Runkle 1991; Yamamoto 1992; Jans et al. 1993). In old-growth forest, canopy gaps have been revealed as an important factor in stand dynamics, especially when large-scale disturbances are absent (Clebsch

& Busing 1989; Lorimer 1989). Our estimate of canopy forest in the gap phase is therefore quite remarkable. Factors causing the low rate of canopy forest in the gap phase could include the virtual absence of hurricanes, uncommon larger gaps (> 75 m^2), low stature of this forest, low rate of fires and the lack of intense insect attacks. This result could suggest that the dynamics of laurel forests are not strongly influenced by canopy gap processes.

The mean gap size in the laurel forest was in the range reported in some reviews (Runkle 1991; Yamamoto 1992). Small gaps (< 10 m^2) were an important component of canopy disturbances but their effects on regeneration are minor because such small gaps were often closed by branches of neighbouring trees.

Among gaps larger than 10 m^2, the frequency distribution of gap sizes points out a negative relationship between number of gaps and size class (small gaps were more common), that is a general pattern followed for other forests (Runkle 1991; Yamamoto 1992; Jans et al. 1993; Yavitt et al. 1995). A low number of larger gaps (> 75 m^2) is an important characteristic, since larger gaps have higher light and heat inputs during mid-day than do smaller gaps and they also have a larger proportion of their total area situated away from the edge (Brandani et al. 1988; Denslow & Gómez-Díaz 1990). Smaller gaps also reduce the probability of shade-intolerant species regeneration (Yamamoto 1992). The range of variation in gap size was small and the distribution of total area per size class was similar to the distribution of the number of gaps per class size as a result of the negative relationship of gaps and size class.

The density of the different regeneration classes followed a similar pattern in the different areas of the gaps and control plots. Shade-tolerant species – *Laurus azorica*, *Viburnum tinus* and *Prunus lusitanica* – dominated in all regeneration classes and areas indicating a low effect of the gap on the composition of regeneration. Suckers composed the regeneration class with the highest densities with respect to other regenerative classes in expanded gap, gap transition and control areas. These high densities point to the importance of asexual regeneration in the laurel forest. It was common that suckers of the gap-maker were the first established stems to occupy the gap.

Only two species showed significant differences in their regeneration densities in gap projection and/or gap transition with respect to the control areas. Saplings densities of *Laurus azorica* were significantly higher in gap projection than in control areas. Because the trees, seedlings, saplings and suckers of this shade-tolerant species were abundant in the forest, this species often has saplings available that can successfully occupy the newly opened area. *L. azorica* was the only species that showed a positive effect of the gap projection on its sapling densities (with respect to the control areas). The seedling densities of *L. azorica* and *Viburnum tinus* were significantly lower in the gap projection. We suspect that high light levels have a negative effect on the germination of this species. Suckers of *L. azorica* present a significantly lower density in gap projection compared to control areas. We related this to the small area of the gap and to the low number of gap-makers of *L. azorica*.

There was a positive effect of gap transition areas on the densities of saplings and suckers of *Laurus azorica* and *Viburnum tinus*. The possible extra light input (not as much as in the gap projection) is assumed to be beneficial for these species. Seedling densities of *L. azorica* were significantly higher in gap transition but lower for *V. tinus*. It is likely that the conditions of the gap transition area are favourable for the germination of *L. azorica* but not for *V. tinus*. The latter species is shade-tolerant and very rarely reaches the canopy. Conditions found in gap projection and gap transition areas could hinder its germination. *L. azorica* is a shade-tolerant species, but gaps could be considered a positive disturbance for this species, which could explain its dominance in this laurel forest.

The importance of treefall gaps in the maintenance of shade-intolerant or pioneer species has been well documented (Washitani & Takenaka 1987; Clebsch & Busing 1989; Ohkubo et al. 1996; Goldblum 1997). Our analysis revealed that only shade-tolerant species showed differences in their densities in the gap with respect to the control plots. Although *Erica arborea*, *Myrica faya* (shade-intolerant) and *Ocotea foetens* (shade-tolerant) did not have regeneration in control plots, this result can not be extrapolated because these species appeared in a low number of gaps (3, 2, and 1, respectively). We can not assume that the environmental heterogenity provided by tree fall increases tree species diversity (Whitmore 1989; Alvarez-Buylla & García-Barros 1991). The total density of regeneration in gaps was higher than in the controls, but with a high variability. We could not find a significant effect of the gaps on the density of the regenerative stems as has been convincingly reported for other forests (Hubbell & Foster 1986; Cho & Boerner 1991).

The composition of gap projection, expanded gap and control areas was not discriminated in the CCA. We assume that the composition of the areas is not different and the variability has to be related to natural heterogeneity.

In other forests single tree-gaps dominate (Spies et al. 1990; Cho & Boerner 1991; Yamamoto 1993; Green 1996). We found that 95 % of the gaps in this forest were produced asynchronously by more than one gap-maker. The different state of decomposition of the gap-makers in each gap was evident. Asexual regeneration in the laurel forest results in clumped trees sharing the same root system (Fernández-Palacios et al. 1996). When one of these trees falls, it drags the rest of the clump down allowing the formation of a large gap (> 10 m^2). Due to the small stature of the trees of the forest, gaps greater than 10 m^2 with simple gap-makers are rare.

We have tested the possibility that some species are more likely to be gap-makers based on density and basal area of control plots. The results (Fig. 2) revealed that *Prunus lusitanica* has a strong tendency to be a gap-maker while *Laurus azorica* and *Ilex canariensis* were less likely than expected to be gap-makers. Short-lived species have a higher understorey density and are significant gap makers (White et al. 1985). In our study *L. azorica* and *Viburnum tinus* dominated the understorey, while *L. azorica* participated in fewer gaps than expected and the number of gap-makers of *V. tinus* was not significantly different from that expected.

Although *P. lusitanica* had high regeneration densities and was a remarkable gap-maker, in the absence of growth data, we cannot generalize the same pattern in the laurel forest. In other forests it has been demonstrated that wood properties could determine the probability of a species to be a gap-maker (Putz et al. 1983; Arriaga 1988). However, we think that the high capacity of *P. lusitanica* to reproduce by suckers destabilizes the root systems and could produce changes in the center of gravity that make the tree susceptible to falling at low wind velocities. This supports the idea that indicate asymmetric branch growth increases the probability of tree fall (Young & Perkocha 1994). Moreover, *P. lusitanica* remains alive after falling. In our study, tree fall predominantly involves uprooting (maintaining the connection of root system-canopy of the tree) and small branches start to grow perpendicular to the surface. These branches are much more competitive (bigger size, well established roots) than seedlings or saplings and are more likely to reach the canopy. This ecological strategy assures the individuals continuity in the forest stand. *Ilex canariensis* and *Laurus azorica* also use asexual reproduction, but not to the same degree as *P. lusitanica* and the mild weather on the islands makes falling of these trees unlikely. When we tested the differences between expected and observed basal area per species and per gap, *Erica scoparia* showed a significantly lower tendency to be a gap-maker, but the null hypothesis is not rejected as strongly as for the other species (Fig. 2).

The results indicate that gaps do not affect the dynamics of the laurel forest as much as in other temperate and tropical forests. This conclusion is supported by the absence of large natural gaps, the lack of differences in the regeneration between gap projection, expanded gap and control areas and the non-significant effect of the gap in the germination of shade-intolerant species. The laurel forest is an evergreen forest with low stature, therefore the contrast between gap and non-gap conditions are not as distinct as in other forests. Also, the high rate of asexual regeneration may be another factor explaining the small part of the canopy in the gap phase. Suckers of gap-makers have higher competitive ability to occupy the new open area because they are in the most favourable position and because, in general, clonal stems grow faster than seedlings (Fenner 1985). In the laurel forest, the effect of gaps on the dynamics of some species is important, but this disturbance is not sufficient to explain the maintenance of biodiversity and dynamics of the forest community.

Intensive work in large gaps is necessary to reveal the effect of this disturbance in the species composition and identify guilds of shade-tolerant and shade-intolerant tree species. Although the remaining laurel forest is well conserved, we think that short but intense human disturbance (cutting small areas for agriculture use or firewood) allowed the establisment of shade-intolerant species at different points inside the forest. In order to understand the laurel forest dynamics we need to consider the anthropogenic effects – which have been intensive since the arrival of Europeans to the island, five centuries ago (Parsons 1981).

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