## ORIGINAL PAPER

# Treefall gaps and regeneration composition in the laurel forest of Anaga (Tenerife): a matter of size?

José Ramón Arévalo · José María Fernández-Palacios

Received: 27 April 2005/Accepted: 7 April 2006/Published online: 12 May 2006 © Springer Science+Business Media B.V. 2006

Abstract The size of treefall gaps is an important determinant of regeneration composition in tropical and temperate forests. Preliminary studies in the laurel forest of Tenerife have shown that small gaps  $(<100 \text{ m}^2)$  were the most numerous. However, due to this small size, no significant differences were found between regeneration in gaps and regeneration below the canopy. Because infrequent large gaps (>100 m<sup>2</sup>) are present in the laurel forest, we analyzed the regeneration in these large uncommon gaps, considering their potentially important role in the dynamics of the system. Our main hypothesis is that large gaps are important disturbance to ensure the regeneration and stablishment of shade intolerant species. Only five gaps larger than  $100 \text{ m}^2$  (ranging from 125–268 m<sup>2</sup>) were found in the study area. Data from a further 20 small gaps  $(<100 \text{ m}^2)$ , analysed in a previous study, was also included. Control plots were examined close to the gaps in order to determine regeneration below the closed canopy. We did not find a significant difference between regeneration density in the gaps  $(<100 \text{ m}^2)$  and regeneration below the canopy in the control plots. Contrary to our expectations, regeneration was lower in the large gaps than under the canopy. The open canopy in the large gaps increases light intensity, and has a negative effect on the germination and growth of shade-tolerant tree species like *Viburnum tinus* (although non-statistically significant); however, the increase in light intensity is not sufficient to stimulate the germination of shade-intolerant tree species. The effects of treefall gaps in the dynamics of the laurel forest of Anaga should be not considered as significant in comparison to other factors such as human disturbances or infrequent disturbances (land slides or hurricanes).

**Keywords** Anthropogenic disturbances · Forest dynamics · Gap-theory · Shade-intolerant species

#### Introduction

Treefall gaps produce a cyclic phenomenon known as gap dynamics (sensu van der Maarel 1988). This phenomenon can explain species regeneration (Hartshorn 1980), survival (Hubbel and Foster 1986; Runkle 1990) and many other aspects of the structure of a forest (Runkle 1991). However, some authors note that it is not possible to generalize about the role of treefall gaps in forest dynamics (Denslow 1987; Kapos et al. 1990), and the paradigm of gap/non-gap does not help to explain species replacement (Arévalo and

J. R. Arévalo (🖂) · J. M. Fernández-Palacios Departamento de Ecología, Universidad de La Laguna, La Laguna 38206, Tenerife, Spain e-mail: jarevalo@ull.es

Fernández-Palacios 1998; Midgley et al. 1995; Lieberman et al. 1989).

Studies carried out in the laurel forest of Anaga revealed that gaps do not affect the dynamics of the laurel forest as much as in other temperate and tropical forests due to the small size of natural gaps and the lack of differences between regeneration in gaps and under closed canopy (Arévalo and Fernández-Palacios 1998). The majority of the gaps found in the laurel forest were small (below  $100 \text{ m}^2$ ). Due to the design of the experiment, large gaps were not used in the study. However, large gaps are present in the laurel forest.

Others have shown that gap size affects the processes associated with the gap dynamic phenomenon (Denslow and Gómez-Díaz 1990; Yamamoto 1992). Larger gaps receive greater light intensity and caloric energy (Chazdon and Fetcher 1984; Chazdon et al. 1999), and they also encompass a larger area in the gap with no edge effects (Brandani et al. 1988; Denslow and Gómez-Díaz 1990), enabling shade intolerant species to germinate and establish (Yamamoto 1992; Gray and Spies 1996). Our hypothesis is that occasional large gaps in the laurel forest explain the presence of shade-intolerant species in the canopy of the laurel forest, and that regeneration density in large gaps differs significantly from that found under closed canopies, in contrast with previous research done with gaps of less than  $100 \text{ m}^2$ . We also hypothesize that those gaps >100 m<sup>2</sup> affect the species composition of seedlings, saplings and suckers established in the area of the projected gap.

The results of this study will be of interest in determining the role of gaps in the laurel forest. These results will also be useful in the design of restoration programs for disturbed laurel forest (i.e., indication of the most appropriate species for plantation) and the conservation of the 10% that remains in the Canary Islands.

## Material and methods

Study site

The study was conducted in the Anaga Rural Park in the northeast of Tenerife, Canary Islands

(28° 19' N, 16° 34' W). The park encompasses a 7 -8 million year old basaltic massif (Ancochea et al. 1990) covering some 130 km<sup>2</sup>. The park represents 7% of Tenerife's total surface area. We selected two sites in the park as representing the best-conserved 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 15th century (Parsons 1981). Today, only 10% of the forest remains. It has enjoyed formal protection since 1988, and currently experiences less human disturbance and no reduction in area. No data is available concerning the precise age of the forest, 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 the deficient protection schedule applied at the time, and the fact that it was a public area.

The maximum annual precipitation of the park is 900 mm, but it can be twice this level if we take fog drip into consideration (Kämmer 1974). The mean annual temperature is close to 15°C with minimal annual and daily fluctuations. There are no frost events. Two seasons, winter and summer, can be differentiated but differences between the two most extreme months tend to be slight (differences between the averages of the extreme months: 8°C, 5% relative humidity and 100 mm rainfall) (Ceballos and Ortuño 1974). The soils have been classified as Entisol order, suborder Orthens, and are typical of high slope areas. They maintain a high level of humidity due to hydrate aluminum silicates, and have a thick A horizon (Fernández-Caldas et al. 1985). The soil has a high organic content (~ 10%) and pH is around 5.5 (Fernández-Palacios and Arévalo 1998).

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 basins' edges. 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 on forest ridges, *L. azorica* in mesic zones and *E. arborea* in more disturbed areas (Ministerio de Agricultura (ICONA) 1973). Further information on stand composition, structure and environment in the study sites can be found in Fernández-Palacios et al. (1992), Arévalo (1998) and Arévalo and Fernández-Palacios (2003).

## Data collection

During the spring 1996, we searched the canopy of the laurel forest of Anaga (approximately 2000 ha) for gaps larger than 100 m<sup>2</sup>. Because the canopy of the laurel forest is around 10 m high, this size of gap is large enough to affect environmental conditions in the area affected by the opening. All gaps found over that size were analyzed. We interviewed inhabitants of the area and forest service members to obtain information about the gaps. Only gaps with no evidence of human disturbance or anthropogenic intervention were included in the study.

The area of the vertical projection of those canopy openings larger than 100 m<sup>2</sup> (hereafter gap) was estimated from a scale map drawn using the distances from the center of the gap to the perimeter along eight compass headings (0, 45, 90, 135, 180, 225, 270 and 315 degrees). We determined the size of the opening at a height of 10 m due to the stature of the forest. This is a more appropriate method of estimating the area when gaps are of irregular shape (Runkle 1992) and as accurate as others recent develop methods (Kneeshaw and Bergeron 1998). Although Green (1996) remarked that this method of measuring gaps could underestimate areas by 10-20%, we used it in order to be able to compare our data with that of forests described using similar methods (Jans et al. 1993; Meer and Bongers 1996).

We determined the gap-maker's species, height, diameter at breast height (dbh), and direction of fall. We also noted whether the gap-maker was uprooted and alive. The slope, orientation, UTM coordinates and altitude of each gap were recorded. All seedlings, saplings and suckers were counted. Seedlings were identified as individuals less than 15 cm tall because the majority of tree species of less than 1 year old do not exceed 15 cm. Saplings were defined as over 15 cm high and less than 5 cm dbh. Suckers were the products of asexual reproduction, with the same origin as the parent tree. All trees found in this study form suckers (Arévalo 1998).

A 100 m<sup>2</sup> control plot (hereafter forest understory 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 with similar topographical and orographical characteristics to those of 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<sup>2</sup> subplot located in a corner chosen at random.

We randomly located 80 plots (2500 m<sup>2</sup> each) and checked the canopy for gaps larger than  $10 \text{ m}^2$ . These gaps were analysed using the same methodology. More information about the small these gaps can be found in Arévalo and Fernández-Palacios (1998).

#### Data analysis

In order to test for significant differences between the regeneration density (seedlings, saplings and suckers) of functional groups (tolerant, mid-tolerant and intolerant species) in control and gaps (>100 m<sup>2</sup>) we used the non-parametric Wilcoxon Rank Sum W test (in this case for n = 5 and P < 0.05).

We compared the total regeneration density (adding seedlings, saplings and suckers, once all the densities had been normalized to  $100 \text{ m}^2$ ) between large gaps (> $100 \text{ m}^2$ ) and their control plots with a random pair *t*-test (P > 0.05, n = 5, Edgington 1985). Non-normal errors made this test suitable (it was not possible to discriminate between regeneration classes because many of the species did not have individuals in all size classes).

The species composition of large gaps  $(>100 \text{ m}^2)$  and control plots was analysed using a CCA (Canonical Correspondence Analysis; ter Braak 1986). In the CCA we used an environmental matrix with only one dummy variable that

represented whether the sample was a control or a gap plot. Because there is only one explanatory variable, there is only one CCA axis. Testing the eigenvalue of the axis with a Monte Carlo Test (P < 0.05, 200 iterations; Sóbol 1983) we can infer the differences between species composition in control plots and gaps. This use of CCA has been successful in the past to analyse differences in the species composition of plots based on a single dummy variable (Arévalo et al. 1999, 2001).

We used DCA (Hill and Gauch 1980) to analyse the species composition of the gaps in addition to the 20 gaps of less than 100 m<sup>2</sup> that were analysed in a previous study. The coordinates on the first DCA axis for each gap number and its corresponding size were correlated using the non-parametric Spearman Rank correlation coefficient and tested for the significance (P < 0.05).

We performed all multivariate analysis with the CANOCO package (ter Braak and Šmilauer 1998) and tested the eigenvalue of the axis with Monte Carlo permutation tests. The statistical methods used follow Zar (1984) and were implemented using the SPSS statistical package (SPSS 1997).

## Results

We found only five gaps larger than  $100 \text{ m}^2$  in our analysis of the whole of the laurel forest canopy. The gap projection size was between 125 m and 268 m. Features of the gaps indicated that they were produced more than 2 years before our research was carried out (Table 1).

Eleven species occurred in the forest understory plots. Forest understory plots were dominated by *Laurus azorica* and *Prunus lusitanica* (both comprised more than 50% of the total basal area and density). *Erica scoparia* and *Ocoetea foetens* also had high density and basal area in the control plots (Table 2).

We found a total of 13 regenerated species in the study, of which 4 are shade tolerant (*Laurus azorica*, *Viburnum tinus*, *Ocoetea foetens* and *Prunus lusitanica*), 3 mid-tolerant (*Heberdenia excelsa*, *Picconia excelsa* and *Rhamnus glandulosa*) and 6 shade intolerant (*Erica arborea*, *E*. scoparia, Ilex canariensis, I. perado, Euphorbia mellifera and Myrica faya) (Arévalo 1998). The statistical test revealed non-significant differences between forest understory plots and gaps when we compared densities of these functional groups (for the three regeneration categories).

When we compared regeneration densities of the species (using the random pair *t*-test) between gaps and forest understory plots, again, we did not find significant differences.

Sapling regeneration in the forest understory plots was dominated by *Heberdenia excelsa* and *L. azorica*, while seedlings were dominated by *L. azorica* and *Ilex perado. Prunus lusitanica* was the dominant sucker (Table 3).

There were also 11 species in the gap projections. Seedlings were dominated by *Heberdenia excelsa*, while *Laurus azorica* dominated the saplings, and *L. azorica* was again the dominant sucker (Table 3). Density values in the gap projections were lower than in the control plots, but they varied considerably.

The most common gap-maker was *Prunus* lusitanica, followed by *Erica arborea* and *Ilex* 

Table 1 General information about the gaps

Gap number	Altitude (m)	Slope (°)	Exposition	Projected area (m <sup>2</sup> )
L-1	745	35	NE	125
L-2	770	40	Ν	190
L-3	890	40	NO	135
L-4	950	55	Ν	152
L-5	975	50	NE	268

**Table 2** Mean density and basal area of trees in five forest understory plots  $(100 \text{ m}^2)$ 

Species	Density (ind./ha)	Basal area (m <sup>2</sup> /ha)
Erica arborea	17.77 (21.77)	0.74 (0.93)
Erica scoparia	440.00 (624.82)	4.90 (6.67)
Heberdenia excelsa	213.33 (327.08)	1.47 (2.82)
Ilex canariensis	264.44 (419.07)	2.14 (2.45)
Ilex perado	84.44 (103.66)	1.43 (1.81)
Laurus azorica	722.22 (464.97)	12.3 (8.42)
Myrica faya	44.4 (68.85)	2.06 (3.61)
Ocotea foetens	160.00 (213.33)	3.66 (5.76)
Picconia excelsa	97.77 (154.98)	0.25 (0.31)
Prunus lusitanica	686.66 (650.33)	6.74 (5.84)
Viburnum tinus	137.77 (34.85)	0.60 (0.58)

Standard deviations are given in parentheses

Species	Forest underst	ory plots		Total	Gap			Total
	Seedlings	Saplings	Suckers		Seedlings	Saplings	Suckers	
Erica arborea	0.27 (0.53)	I	I	0.27 (0.53)	1.19 (2.39)	0.82 (1.64)	0.26 (0.53)	2.27 (3.93)
Erica scoparia	, , ,	I	4.60 (9.20)	4.60(9.20)	1.30(2.34)	0.53(2.61)	Ì	1.92(3.35)
Heberdenia excelsa	4.31 (6.48)	16.00 (19.43)	1.47(2.08)	21.77 (24.24)	Ĭ	0.15(0.30)	0.44(0.89)	0.59(1.18)
Euphorbia mellifera	, I	I		, I	6.03 (6.43)	1.03(1.74)	, , 	7.05 (7.70)
llex canariensis	I	I	I	I	Ì	, I	0.22 (0.45)	0.22(0.45)
llex perado	2.36 (3.88)	29.60 (49.81)	4.44 (6.26)	36.40 (59.79)	1.00(1.81)	1.50 (2.07)	11.05 (22.11)	13.54 (25.81)
Laurus azorica	3.86(5.56)	29.60 (25.50)	4.59(3.84)	16.70 (15.24)	0.51(0.64)	3.69(4.37)	0.73(1.02)	4.93 (6.00)
Myrica faya	, I	ľ	0.82(1.63)	0.82(1.63)	, I	, I		
Ocotea foetens	I	I	0.89(1.78)	0.89(1.78)	I	0.53(1.05)	3.51 (6.48)	4.03 (7.53)
Picconia excelsa	I	0.40(0.80)		0.40(0.80)	I	0.13(0.26)		0.13(0.26)
Prunus lusitanica	I	0.80(1.60)	18.87 (16.42)	19.66 (17.12)	I	, I	38.72 (27.38)	38.72 (27.38)
Rhamnus glandulosa	1.78 (2.20)	2.40(4.80)	, , 1	4.17 (6.54)	1.33 (1.37)	I	,	1.33 (1.37)
Viburnum tinus	2.84 (3.53)	15.20(6.40)*	2.44 (1.35)	20.48 (12.73)	2.03 (2.72)	3.28 (4.47)	2.21 (2.66)	11.20 (9.75)
Total	15.41 (11.77)	89.60 (18.84)	38.50 (17.36)	143.49 (100.66)	13.38 (10.90)	11.76 (10.17)	57.16 (45.85)	82.27 (55.83)

perado (47%, 17% and 14%, respectively). The majority of the gap-makers were found alive (they remained alive and producing green leaves and even fruits long time after falling), except for *E. arborea*, *E. scoparia* and *Myrica faya*, and they are all considered shade intolerant species (Fernández-Palacios and Arévalo 1998) (Table 4).

The CCA analysis of the five gaps and five control plots (based on density/100 m<sup>2</sup>) using "gap projection/control" as the only dummy variable in the environmental matrix, revealed that the eigenvalue of CCA axis I was not significant (P < 0.05) in the explanation of scores of the plots along the axis. This result was the same for seedlings (eigenvalue: 0.239, percentage of variability explained: 15.2%), saplings (eigenvalue: 0.173, percentage of variability explained: 9.1%) and suckers (eigenvalue: 0.172, percentage of variability explained: 11.6%).

The DCA ordination of the seedling, sapling and sucker composition is shown in Fig. 1, 2, and 3, respectively. In this ordination we used the species composition in the 20 gaps analysed in the paper by Arévalo and Fernández-Palacios (1998) together with the information from the five large gaps found in this study. Using these data we can reveal differences in species composition base in the size of the gap. The ordination of seedlings indicated some discrimination for large gaps with respect to the other gaps, with a clear presence of the shade intolerant species Erica scoparia and Erica arborea. The ordination of suckers and saplings did not show any clear pattern in relation to the size of the gap. We found no significant correlations between the size of the gap and the coordinate of the gap on the DCA axis I (Spearman correlation coefficients 0.22, 0.13 and 0.07 for seedlings, saplings and suckers, respectively; nonsignificant at  $\alpha = 0.05$ , n = 24 or 23; some gaps did not have any presence of saplings or seedlings), indicating that DCA axis I did not discriminate the gaps' composition as a function of size.

#### Discussion

Total densities showed higher values in control plots than in the gap projections (using only the five large gaps). These results do not tally with

Especies	Number of gap-makers	% alive	% uprooted	DBH (cm)	Height (m)
Erica arborea	15	0	100	12.74 (3.84)	8.95 (2.45)
Erica scoparia	6	0	66.6	16.02 (7.99)	9.10 (1.88)
Euphorbia mellifera	2	100	100	26.58 (4.30)	11.35 (0.35)
Ilex canariensis	1	100	100	8.59	6.80
Ilex perado	12	91.6	91.6	10.94 (4.37)	9.22 (2.19)
Laurus azorica	4	25	75	19.58 (7.41)	11.83 (2.21)
Myrica faya	1	0	100	30.24	13.50
Ocotea foetens	1	0	100	7.96	1.60
Prunus lusitanica	39	89.7	82.1	15.92 (5.89)	10.58 (2.35)
Rhamnus glandulosa	1	100	100	16.23	11.40
Viburnum tinus	4	100	100	4.77 (2.39)	7.80 (1.90)

Table 4 Summary of gap-making characteristics in the five gaps larger than 100 m<sup>2</sup> found in the laurel forest of Anaga

DBH and height are given as means and standard deviations (in parentheses)

results found in other studies (White et al. 1985) or when smaller gaps were analysed (Arévalo and Fernández-Palacios 1998). We suggest that when a large gap occurs, there is a higher disturbance of the soil's organic layer (tipup mounds), decreasing or increasing (depending on the species) the germination capacity of species in the soil seed bank.

However, when species density was compared between gap and control plots, our analysis revealed non-significant differences. When we aggregated the species in functional groups (shade tolerant, mid tolerant and shade intolerant), we once again found no significant differences in density between control plots and gaps.

We suggest that increased light intensity and the change in other environmental factors associated with gap projections (increase in humidity that we found on some days to be around 20% less in the gaps) seem to have little negative effect on these shade-tolerant species, and no significant effect on germination or establishment of shade intolerant species. Although three species showed higher densities in gaps than in control plots (Erica arborea, Prunus lusitanica and Ocotea foetens), the differences were not statistically significant (P > 0.05, n = 5). Also Euphorbia mellifera and Ilex canariensis appeared only in gaps, but E. mellifera was only found in one plot and I. canariensis only appeared as suckers (Table 3).

With respect to species composition, some patterns were apparent in the ordination of the seedlings, such as the presence of shade-intolerant species in large gaps, and their absence in smaller gaps. However, this tendency was not supported statistically. The presence of shade intolerant species in these gaps can not explain their presence in the canopy of the laurel forest. The same results were not found for saplings, indicating that even when germination is possible, establishment is not necessarily guaranteed. Sucker composition was related to the composition of the canopy where the gap occurred.

Ordination of suckers showed a larger DCA axis I (4.5 units) than that of seedlings or saplings. Because the length of this axis is related to the  $\beta$ -diversity of the samples analysed (ter Braak 1995), we suggest that asexual regeneration is one of the most important factors for the maintenance of species richness in this forest. These results agree with those of other studies that point to the importance of asexual regeneration in this forest (Arévalo et al. 1999). The species composition in the immediate area of the gap can be considered the most important factor determining the species composition in the gap projection, as has been previously suggested in other studies (Lieberman et al. 1989).

When we evaluated the effect of gap size on the ordination of species composition, we found that it was not significant, despite the fact that several studies have shown the importance of gap size for regeneration in temperate and tropical forests (Brokaw 1985; Runkle 1998; Schetnizer and Carson 2001).

With these results we cannot accept that largegap dynamic processes will suffice to ensure



DCA - Gap number and seedling species coordinates

Fig. 1 DCA axis I and II for seedling regeneration species and gap number coordinates (eigenvalues were 0.806 and 0.315, respectively and the cumulative percentage variance of species data of both axis was 57.1%). Large gaps are numbered from gap L1 to gap L5, while small gaps (< 100 m<sup>2</sup>) are numbered from gap1 to gap20. For gap12, species composition was not sampled for any category. Acronyms for Fig. 1, 2 and 3—Apolbarb: Apollonias

maintained species richness in the laurel forest, despite some results pointing in that direction (importance of shade intolerant species and low barbujana; Ericarbo: Erica arborea; Ericscop: Erica scoparia; Euphmell: Euphorbia mellifera; Hebeexel: Herberdenia excelsa; Ilexcana: Ilex canariensis; Ilexpera: Ilex perado; Laurazor: Laurus azorica; Myrifaya: Myrica faya; Ocotfoet: Ocotea foetens; Picoexce: Picconia excelsa; Prunlusi: Prunus lusitanica; Rhamglan: Rhamnus glandulosa; Vibutinu: Viburnum tinus

densities in gap projection of shade-tolerant species). Although the remaining laurel forest is well conserved, human disturbance (cutting small



**Fig. 2** DCA axes I and II for sapling regeneration species and gap number coordinates (eigenvalues were 0.503 and 0.316, respectively and the cumulative percentage variance

areas for agriculture or to use the wood as firewood) were particularly intense until 56 years ago (Parsons 1981; Galván 1993). Environmental heterogeneity is another factor that should be considered important in the maintenance of spe-

of species data of both axes was 36.4%). Gap L-1 did not show sapling regeneration

cies richness since some rocky areas and areas with a reduced organic soil layer can only be colonized by shade-intolerant species such as *Erica arborea* and *Erica scoparia* (Fernández-Palacios and Arévalo 1998). Because native inhabitants of the island



#### DCA - Gap number and sucker species coordinates

**Fig. 3** DCA axes I and II for sucker regeneration species and gap number coordinates (eigenvalues were 0.729 and 0.576, respectively and the cumulative percentage variance of species data of both axis was 34.7%)

did not affect the dynamics of the laurel forest (García 1989), environmental variability (as well as some infrequent disturbances such as hurricanes and diseases) was the only mechanism important in the maintenance of species richness before European colonization.

In a previous study on gap dynamics and forest structure, similar results were obtained, and it was suggested that it is necessary to sample larger natural gaps in order to make inferences about how gaps affect forest dynamics (Arévalo and Fernández-Palacios 1998). We conclude that natural gaps (of any size) have a very low impact on the ecological processes and the maintenance of tree species richness in the laurel forest of Anaga.

Acknowledgments This work is part of a research project on laurel forest dynamics (No. 95 6219 05, LIFE projects) supported by the Canarian Government (Consejería de Política Territorial) and the European Union. We thank the fine stuff of the Parque Rural de Anaga for granting permission to conduct this study. And support of the project. We also thank Jerry Husak (Oklahoma State University) for his valuable comments and edition of this manuscript, which has been translated into English by Heather Adams, ULPGC, Spain.

### References

- Ancochea E, Fuster JM, Ibarrola E, Cendrero A, Coello J, Hernán F, Cantagrel JM, Jamond C (1990) Volcanic evolution of the island of Tenerife (Canary Islands) in the light of new K-AR data. J Volc Geotherm Res 44:231–249
- Arévalo JR (1998) Organización espacial y temporal de la laurisilva de Anaga-Tenerife. Islas Canarias. Ph.D. dissertation. Universidad de La Laguna. La Laguna. Spain
- Arévalo JR, Fernández-Palacios JM (1998) Treefall gap characteristics and its influence on regeneration in the laurel forest of Tenerife. J Veg Sci 9:297–306
- Arévalo JR and Fernández-Palacios JM (2003) Spatial analysis of trees and regeneration of *Laurus azorica* in a laurel forest in Tenerife. Plant Ecol 163:1–10
- Arévalo JR, Fernández-Palacios JM, Palmer MW (1999) Tree regeneration and future dynamics of the laurel forest on Tenerife, Canary Islands. J Veg Sci 10:861–868
- Arévalo JR, Fernández-Palacios JM, Jiménez, MJ and Gil P (2001) The effect of fire in the understory of two reforested stands of *Pinus canariensis*. Tenerife Canary Islands. For Ecol Manage 148:21–29
- Brandani A, Hartshorn GS and Orians GH (1988) Internal heterogeneity of gaps and species richness in Costa Rican tropical wet forest. J Trop Ecol 4:99–119
- Brokaw NVL (1985) Gap-phase regeneration in a tropical forest. Ecology 66:682–687
- Ceballos L and Ortuño F (1974) Vegetación y flora forestal de las Canarias Occidentales. 2th ed. Cabildo Insular de Tenerife, Santa Cruz de Tenerife
- Chazdon RL and Fetcher N (1984) Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. J Ecol 72:553–564
- Chazdon RL, Colwell RK and Denslow JS (1999) Tropical tree richness and resource-base niches. Science 285:1459
- Denslow JS (1987) Tropical rainforest gaps and tree species diversity. Annu Rev Ecol Syst 18:431–451
- Denslow JS and Gómez-Díaz AE (1990) Seed rain to trefall gaps in a neotropical rain forest. Can J For Res 20:642–648
- Edgington ES (1985) Randomization tests. Marcel Dekker, Inc. New York
- Fernández-Caldas E, Tejedor M and Quantin P (1985) Los suelos volcánicos de Canarias. Serv Public Univ. La Laguna, La Laguna
- Fernández-Palacios JM and Arévalo JR (1998) Tree strategies regeneration of the trees in the laurel forest of Anaga Tenerife. Plant Ecol 137:21–29
- Fernández-Palacios JM, López R, Luzardo C and García J (1992) Descripción ecológica y evaluación de la producción primaria neta de cuatro estaciones representativas de los ecosistemas más característicos de Tenerife (Islas Canarias). Studia Oecologica 9:105–124
- Galván AD (1993) Los inicios de la deforestación de la isla de Tenerife y las ordenanzas del Cabildo sobre

madera. Instituto de Estudios Canarios (Stranae Emmanuellae Marrero Oblata):373–389

- García M (1989) El bosque de la laurisilva en la economía guanche Cabildo Insular de Tenerife (Museo Arqueológico) Santa Cruz de Tenerife
- Gray AN and Spies TA (1996) Gap size, within-gap position and canopy structure effects on conifer seedling establishment. J Ecol 84:635–645
- Green PT (1996) Canopy gaps in rain forest on Christmas Island, Indian Ocean: size distribution and methods of measurement. J Trop Ecol 12:427–434
- Hartshorn GS (1980) Neotropical Forest Dynamics. Biotropica 12:23–30
- Hill MO and Gauch H Jr, (1980) Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47–58
- Hubbell SP and Foster RB (1986) Canopy gaps and the dynamis of a neotropical forest. In: Crawley MJ (ed) Plant Ecology. Blackwell, Oxford, pp 77–96
- Jans L, Poorter L, van Rompaey RSAR and Bonger F (1993) Gaps and forest zones in tropical moist forest in Ivory Coast. Biotropica 25: 258–269
- Kämmer F (1974) Klima und Vegetation auf Tenerife, besonders im Hinblick auf den Nebelniedershlag. Scr Geobot 7:1–78
- Kapos V, Pallant E, Bien A and Freskos S (1990) Gap frequencies in lowland rain forest sites on contrasting soils in Amazonian Ecuador. Biotropica 22:218–225
- Kneeshaw DD and Bergeron Y (1998) Canopy gaps characteristics and tree replacement in the southeastern boreal forest. Ecology 79:783–794
- Lieberman M, Lieberman D and Peralta R (1989) Forests are not just swiss cheese: canopy stereogeometry of non\gaps in tropical forest. Ecology 70:550–552
- Midgley JJ, Cameron MC and Bond WJ (1995) Gap characteristics and replacement patterns in the Knysna Forest, South Africa. J Veg Sci 6:29–36
- Ministerio de Agricultura (ICONA) (1973) Inventario Forestal Nacional. Santa Cruz de Tenerife
- Parsons JJ (1981) Human influence in the pine and laurel forest of the Canary Islands. Geogr Rev 71:253–271
- Runkle JR (1990) Gap dynamics in an Ohio Acer-Fagus forest and speculations on the geography of disturbance. Can J For Res 20:632–641
- Runkle JR (1991) Gap dynamics of old-growth eastern forests: management implications. Nat Areas J 11:19– 25
- Runkle JR (1992) Guidelines and sampled protocol for sampling forest gaps. United States Departament of Agriculture, Forest Service General Thechnical Report, PNW\GTR\293
- Runkle JR (1998) Changes in southern Appalachian canopy tree gaps sample thrice. Ecology 79:1768–1780
- Santos A (1990) Bosques de Laurisilva en la región macaronésica. Colección Naturaleza y Medio Ambiente, No. 49, Council of Europe. Strassbourg
- Schnitzer SA and Carson WP (2001) Treefall gap and the maintainence of species diversity in a tropical forest. Ecology 82:913–919

- Sóbol IM (1983) El método de Montecarlo. Editorial Mir. Moscú
- SPSS (1997) SPSS Base 7.5 applications guide/SPSS Inc. Chicago, IL
- ter Braak CJF (1986) Canonical correspondence Analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179
- ter Braak CJF (1995) Ordination. In: Jongman RHG, ter Braak CJF and van Tongeren OFR (eds) Data analysis in community and landscape ecology, Cambridge University Press, Cambridge, pp 78–90
- ter Braak CJF, and Šmilauer (1998) CANOCO reference manual and user's guide to Canoco for Windows: Software for canonical community ordination (version 4). Microcomputer Power. Ithaca NY

- van der Maarel E (1988) Vegetation dynamics: patterns in time and space. Vegetatio 77:7–19
- van der Meer PJ and Bongers F (1996) Patterns of tree-fall and branch-fall in a tropical rain forest in French Guiana. J Ecol 84:19–29
- White PS, McKenzie MD and Busing RT (1985) A critique on overstory/understory comparisons based on transition probability analysis of an old growth spruce-fir stand in the Appalachians. Vegetatio 64:37–45
- Yamamoto SI (1992) The gap theory in forest dynamics. Bot Mag Tokyo 105:375–383
- Zar JH (1984) Biostatistical analysis 2nd ed. Prentice-Hall, Englewood Cliffs NJ