

Seedling bank's structure and dynamic of the relict laurel forest of the Canary Islands

***Fernández-Lugo, S., *de Nascimento, L., *Méndez, J., *González-Delgado, G., **Gomes, E.P.C., *Otto, R., *Arévalo, J.R. and *Fernández-Palacios, J.M.**

Abstract. The structure and species composition of the laurel forest depend considerably on the regeneration strategies of the tree species that make up its canopy. In this study, since regeneration of the climax species takes place primarily by seedlings, we inquire into the seedling bank's temporal dynamic of this community in the Anaga Rural Park (Tenerife). To this end, all seedlings from six 10 m x 10 m plots, were identified and monitored monthly from 2000 to 2003. Two extra samplings were done in November 2005 and 2011. Additional information on adult species and suckers was also recorded. *Laurus novocanariensis* was the dominant seedling species, followed by *Persea indica* and *Picconia excelsa*. More representative canopy tree species were *Erica arborea* and *L. novocanariensis*. Less than 50% of seedlings reach the first year of life and only 10% live until the third year. Survival rates differ significantly between species. The highest survival rates were found for *P. excelsa* and *Rhamnus glandulosa*, which may be explained by its non-pioneer reproductive strategy that implies a permanent seedling bank able to growth under a closed canopy. The highest establishment takes place in summer, the warmest season and when the trade winds reach the greatest intensity. The highest mortality is found in the ~~next season~~, when the rainy season and consequent runoff starts.

Key words: Canarian Laurel forest, Kaplan-Meier survival curves, establishment, mortality

* Island Ecology and Biogeography Group, Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias (IUETSPC), Universidad de La Laguna (ULL), Avda. Astrofísico Francisco Sánchez s/n, 38206 LA LAGUNA (TENERIFE), SPAIN;

** Instituto de Botânica, SÃO PAULO, BRAZIL;


E-mail: sfdezlu@ull.es





Introduction

The Atlantic Laurel forest, present in the Macaronesian oceanic archipelagos of Azores, Madeira and the Canary Islands is considered to be an old relict of the former much wider distributed Palaeotropical Geoflora, which was the main forest type in Central and South Europe as well as in North Africa, during the Tertiary, lasting there until the final deterioration of the climate that reached its zenith in the onset of the Pleistocene Glaciations (MAI, 1989, 1991; POSTIGO MIJARRA *et al.*, 2009; FERNÁNDEZ-PALACIOS *et al.*, 2011). Due to the vertical migration possible in high volcanic islands, and the tampon effect exerted by the ocean, this ecosystem, although in an impoverished version, was able to survive until nowadays in the Atlantic islands. After the onset of the Mediterranean type climate, some 3 My BP, coinciding with the Pleistocene Glaciations, the laurel forest was able to withstand the summer drought imposed by this climate type refuged in the influence area of the trade winds orographic cloud layer, which in the Canaries is distributed among 600 and 1200 m at the windward (northern) slopes of the central (Gran Canaria, Tenerife and La Gomera) and western (La Palma and El Hierro) islands.

Its floristic composition is dominated by palaeoendemic fern and tree species, sharing the distribution of many of the ferns and some of the trees still with Iberia, where they have been able to survive in Pleistocene refugia such as Cádiz, the Algarve, Galician or Cantabrian mountains, constituting the Iberian-Macaronesian floristic element. Within the Macaronesian archipelagos, many tree species are shared by Madeira and the Canaries, whereas the Azores although poor in species due to its isolation, possesses a fair proportion of endemic tree species (Table 1).

Although several works have been published in the last years dealing with the regeneration dynamics of this forest (FERNÁNDEZ-PALACIOS and ARÉVALO, 1998; FERNÁNDEZ-PALACIOS *et al.*, 2004; ARÉVALO and FERNÁNDEZ-PALACIOS, 1998, 2000, 2005, 2007; ARÉVALO *et al.*, 1999, 2007, 2008, 2011, 2012) our knowledge about the real role of the seedling community in the canopy substitution is still very poor. The aim of the present work is to offer some insights in this topic, which are crucial for the reforestation efforts of this unique forest.

 **Table 1** - Distribution and species adscription of the main Macaronesian laurel forest genera. **in bold**, endemic genera.

Tree Genus	Azores	Madeira	Canaries	Iberia
<i>Erica</i>	<i>azorica</i>	<i>maderensis</i>		
platycodon	arborea 			
platycodon	arborea			
<i>Ilex</i>	<i>azorica</i>	<i>canariensis</i>		
perado	canariensis 			
perado	aquifolium			
<i>Laurus</i>	<i>azorica</i>	<i>novocanariensis</i>	<i>novocanariensis</i>	<i>nobilis</i>
<i>Morella</i>	<i>faya</i>	<i>faya</i>	<i>faya</i>	
rivas-martinezii	faya ? 			
<i>Prunus</i>	<i>lusitanica</i>	<i>lusitanica</i>	<i>lusitanica</i>	<i>lusitanica</i>
<i>Vaccinium</i>	<i>cylindraceum</i>	<i>padifolium</i>		<i>several sp.</i>
<i>Euphorbia</i>	<i>stygiana</i>	<i>mellifera</i>	<i>mellifera</i>	
<i>Juniperus</i>	<i>brevifolia</i>	<i>cedrus</i>	<i>cedrus</i>	
Picconia 	<i>azorica</i>	<i>excelsa</i>	<i>excelsa</i>	
<i>Sambucus</i>		<i>lanceolata</i>	<i>palmensis</i>	<i>nigra</i>
<i>Rhamnus</i>		<i>glandulosa</i>	<i>glandulosa</i>	<i>several sp.</i>
<i>Apollonias</i>		<i>barbujana</i>	<i>barbujana</i>	
<i>Heberdenia</i>		<i>excelsa</i>	<i>excelsa</i>	
<i>Ocotea</i>		<i>foetens</i>	<i>foetens</i>	
<i>Persea</i>		<i>indica</i>	<i>indica</i>	
<i>Visnea</i>		<i>mocanera</i>	<i>mocanera</i>	
<i>Viburnum</i>	<i>trelesi</i>		<i>rigidum</i>	<i>several sp.</i>
<i>Frangula</i>	<i>azorica</i>			
<i>Clethra</i>		<i>arborea</i>		
<i>Pittosporum</i>		<i>coriaceum</i>		
<i>Arbutus</i>			<i>canariensis</i>	<i>unedo</i>
Pleioimeris			<i>canariensis</i>	

Material and methods

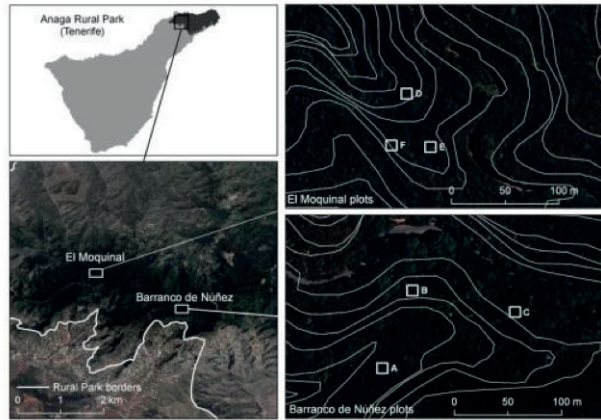


Figure 1 - Map of Tenerife and Anaga Rural Park, showing the different study stations and the plots.

Study site

The study was conducted in the Anaga Rural Park in the northeast corner of Tenerife, Canary Islands ($28^{\circ} 19'N$, $16^{\circ} 34'W$) (Figure 1). The park encompasses a 7-8 million-year-old basaltic massif (ANCOCHEA *et al.*, 1990) covering ca. 130 km², and representing 7% of Tenerife's total area. Tenerife's evergreen laurel forest has been extensively exploited since the arrival of the Europeans in the 15th century (PARSONS, 1981). The 10% of the remaining forest has been formally protected since 1988. Anaga was selected to carry on this study for encompassing the best preserved laurel forest remnants of the island, which occupy around 2000 ha in size, and being the most biodiverse area of the island.

The laurel forest is distributed between 600 and 900 m altitude and, depending on the slope, the canopy is 10-20 m in height. The laurel forest of Anaga contains a total of 19 tree species (SANTOS, 1990). Dominant species include *Laurus novocanariensis*, *Erica platycodon*, *Erica arborea*, *Ilex canariensis*, *Prunus lusitanica*, *Morella faya* and *Viburnum rigidum*. The dominance of a given species depends on site conditions. For example, *E. platycodon* dominates on forest ridges, *L. novocanariensis* in mesic zones and *E. arborea* in more disturbed areas (ANON., 1973).

The annual precipitation of the park reaches 900 mm, but can be twice this amount if fog drip is accounted for (KÄMMER, 1974). The mean annual temperature is close to 15°C with minimal annual and daily fluctuations and no frost events. Two seasons can be differentiated, winter and summer, but in most years differences between the two most extreme months are not great (differences between the averages of the extreme months: 8°C, 5% relative humidity and 100 mm of rain) (CEBALLOS and ORTUÑO, 1976). The soils have been classified in the order Entisol, suborder Orthens.

Sampling design

In the year 2000 we selected two study stations within the Anaga Laurel forest 'El Moquinal' and 'Barranco de los Núñez' (Figure 1) under similar environmental conditions. In each station we located three permanent 10 x 10 m plots. This scale provided a good representation of the vegetation of the area, additionally, a small scale allow a better relation of the results with biological interactions because the environmental gradient is shorter (WIENS, 1989). To record data with a high degree of precision and minimal amount of sampling error, all plots were permanently marked with iron bars and geo-referenced with fixed UTM coordinates.

Within each plot we recorded the Cartesian coordinates (X, Y) of trees, suckers and seedling of each species. We measured the DBH (diameter at breast height) and height of trees and suckers. Each seedling was permanently marked with a label, and establishment and death date were recorded. Sampling was carried out monthly from 2000 to 2003. Two extra samplings were done in November 2005 and 2011.

Statistical analyses

Normality of the data was checked with the Shapiro-Wilk test and the homoscedasticity of the data with a multiple F test. According to exploratory analyses, studied variables were not normally distributed, so non-parametric statistical methods were applied.

To ensure that selected study stations (El Moquinal and Barranco de los Núñez) are comparable in terms of species composition we used the Multiple-Response Permutation Procedure (MRPP) in PC-Ord statistical package (MCCUNE and MEF-FORD, 1995). Relative Sørensen (Bray-Curtis) was used as distance measure because it takes into account both composition (presence-absence of species) and abundance (basal area values).

Survival curves of seedlings were estimated using Kaplan-Meier's method (KAPLAN and MEIER, 1958). Independent analyses were run for the whole seedling bank and for each species seedling bank. Differences in the shape of curves among species were tested by the log-rank test (PYKE and THOMPSON, 1986). Wilcoxon's test was used to detect differences in seedling establishment and mortality between seasons. Analyses were done using SPSS statistical package (SPSS, 1986).

Results

A total of 21,702 seedlings were monitored during the study period. *Laurus novocanariensis* was the dominant seedling species (84% of the seedlings), followed by *Picconia excelsa* (10%) and *Persea indica* (4%). *Viburnum rigidum*, *Apollonias barbujana*, *Rhamnus glandulosa* and *Ilex perado* were also present in the seedling bank, although contributing with less than 2% ~~to the seedling bank~~. More representative canopy tree species, in terms of basal area, were *L. novocanariensis* (13.18 m²/ha) and *Erica arborea* (11.76 m²/ha), followed by *P. indica* (7.86 m²/ha), *I. perado* (7.33 m²/ha) and *Morella faya* (6.69 m²/ha). Other trees contributing to the canopy were *Prunus lusitanica* (5.28 m²/ha), *Ilex canariensis* (3.72 m²/ha), *P. excelsa* (1.48 m²/ha), *A. barbujana* (0.11m²/ha) and *V. rigidum* (0.08 m²/ha). Mean basal area of the plots was 57.99 m²/ha.

Species composition did not differ significantly between study stations (MRPP, $p > 0.05$). Consequently, statistical analyses were applied to the whole data set. Kaplan-Meier curves indicate that less than 50% of seedlings reach the first year of life and only 10% live until the third year. Around 5% of the seedlings survive up to eleven years (Figure 2A). Seedling survival differs significantly among species (Log-rank test, $p < 0.05$). The highest survival rates fell on *P. excelsa* (near 20% of survival after 5 years), *R. glandulosa* (10% of survival after 5 years) and *V. rigidum* seedlings (5% of survival after 5 years) (Figure 2B).

Mean annual establishment was 793 ± 250 seedlings. Mean annual mortality was 602 ± 239 seedlings. Seedling establishment and mortality varied between seasons (Wilcoxon's test, $p < 0.05$). The highest seedling establishment took place in summer (Figure 3A), while highest mortality was found in the next season, autumn (Figure 3B).

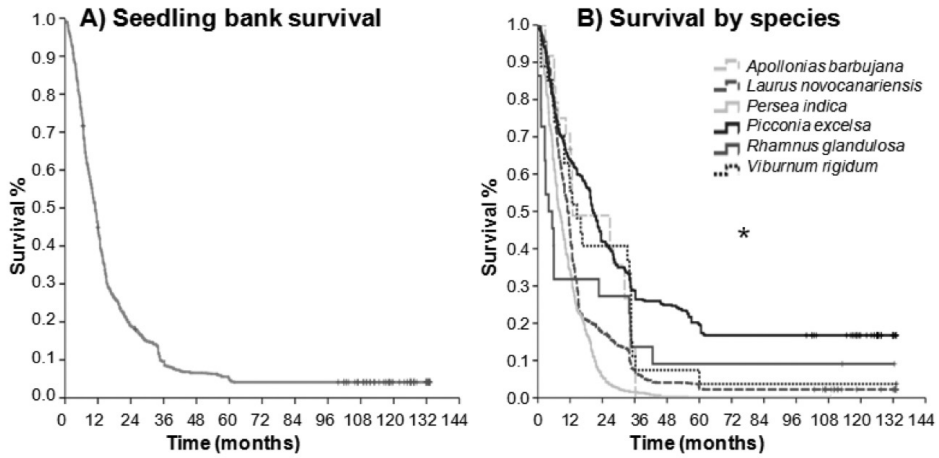


Figure 2 - Kaplan-Meier survival curves for A) the whole seedling bank, B) the seedling bank of each species. *Significant differences among curves (Log-Rank Test, $p < 0.05$).

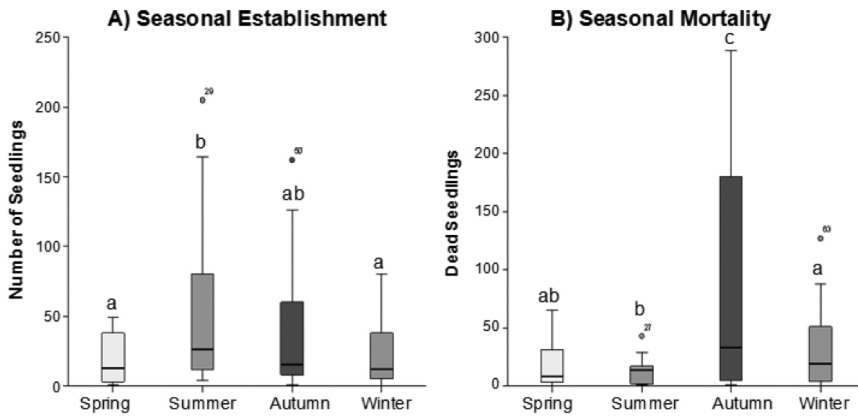


Figure 3 - Seedling bank A) seasonal establishment and B) seasonal mortality. Only those years with a monthly monitoring (2001-2003) were included. Note that graphs have different scales. Bars indicate C.I. at 95%. Different letters above the bars indicate significant differences (Wilcoxon test, $p < 0.05$).

Discussion

Despite the high number of seedlings established during the study period the contribution by species was uneven. *Laurus novocanariensis* seedlings were prevailing over the other tree species which together only accounted for 16% remaining. This superabundance might be related to the dominance of adult *Laurus* trees in the stands; however other trees with similar participation in the forest canopy (*Erica arborea*, *Persea indica*, *Ilex canariensis* or *Morella faya*) appeared with little or no representation in the seedling bank.

The absence of *E. arborea* and *M. faya* from the seedling bank has been previously recorded in the laurel forest, although both species are present as viable seeds on the seed bank (ARÉVALO and FERNÁNDEZ-PALACIOS, 1998; ARÉVALO and FERNÁNDEZ-PALACIOS, 2000). This lack of relationship between the seedling bank and the canopy composition has been explained by different regeneration strategies adopted by tree species within the laurel forest (FERNÁNDEZ-PALACIOS and ARÉVALO, 1998). *E. arborea* and *M. faya* are pioneer species (WHITMORE, 1989) that regenerate primarily by seedlings (although *M. faya* also produces suckers) and are unable to germinate under shady conditions and thus are not present in the seedling bank unless natural or human disturbances increase light conditions in the understory. The occurrence of *E. arborea* and *M. faya* trees in the studied stands indicates a mid-late successional stage of the forest (FERNÁNDEZ-PALACIOS and ARÉVALO, 1998; ARÉVALO *et al.*, 2012).

Non-pioneer species, represented by the four Lauraceae species, show both sexual and asexual regeneration (WHITMORE, 1989) and are able to germinate under shady conditions, obtaining the reserves from their big seeds. As we have observed in our study, Lauraceae species usually display a dense seedling bank; differences in their dominance are, in this case, directly related with their parent trees abundance. Other non-pioneer species relatively abundant on the seedling bank are *P. excelsa*, *V. rigidum* and *R. glandulosa*, in this group asexual regeneration is not common and seeds have short latent periods relaying in the seedling bank for its regeneration (ARÉVALO and FERNÁNDEZ-PALACIOS, 2000). In general we found correspondence between the abundance of trees and seedlings for these species, however is striking that *P. excelsa* is the second species dominating the seedling bank whereas trees of this species are among the less abundant. Based on the measurement around isolated trees from *P. excelsa*, we know that seedlings

reached distances ~~normally~~ further than 30m from the parent tree base (ARTEAGA *et al.*, 2006), thus seeds might have fallen or dispersed from nearby trees outside the plot. Finally, trees adopting a remnant strategy (ERIKSON, 1996), represented in our study by *I. canariensis*, *I. perado* and *P. lusitanica*, are characterized by asexual regeneration (suckers), and therefore seedlings are almost absent in the forest.

Similar average values obtained for the overall establishment and mortality denote a constant turnover entailing the persistence of the seedling bank through time. Summer came out as the best season for germination, very likely due to a combination of suitable environmental conditions (light, temperature and humidity) and fruit production timing. A greenhouse experiment monitoring seed germination from soils collected in the same area also detected higher germination rates in summer (ARÉVALO and FERNÁNDEZ-PALACIOS, 2000). The analysis of fruit fall, in the same site, did not show any seasonal difference in species composition, however, a general trend for almost all the species revealed more fruit production in winter and spring whereas it decreased in summer (ARÉVALO *et al.*, 2007). Accordingly, the season with highest mortality (autumn) follows the season of highest germination (summer), where seedling density has increased and competition processes result in higher mortality (HUTCHINGS, 1997). In addition, recent germinated seedlings are in their most vulnerable stage being threatened by predation, drought events, unusual temperatures or pathogens (CRAWLEY, 1997; KITAJIMA, 2007). Another reason for high mortality during autumn is the occurrence of intense rain episodes that generate water runoff uprooting seedlings (HAMPE and ARROYO, 2002).

Despite the higher values of mortality observed for the study half of the population of seedlings still alive after the first year, which is considered to be the most sensitive life stage for many plant species (AUGSPURGER, 1984; GERHARDT, 1996). Survival probabilities become even lower after three years of life; however, a small proportion of the seedlings can survive for ten or more years within the laurel forest. Shade-tolerant species are able to maintain seedling/sapling banks through long time periods until suitable conditions to promote to adult stages become available; this is known as the Oskar's syndrome (SILVERTOWN, 1982). Other species can grow even under the closed canopy until they reach adult tree sizes. This is the case for the species showing highest survival probabilities in our study (*P. excelsa*, *R. glandulosa* and *V. rigidum*). Many factors may act jointly to increase the chances of seedling survival, such as abiotic factors (water availability, temperature, soil nutrients or litter depth), biotic factors (pathogens, herbivores) or functional traits (seed size, cotyledons morphology, root development, carbo-

hydrate storage or chemical properties) (ALVAREZ-CLARE and KITAJIMA, 2009). A reason for the longer survival of these three species could be related to their regeneration strategy. They all are non-pioneer species mainly relying in the seedling bank for its survival as they do not produce suckers. Another common feature is their relatively large fruit (9-19 cm length and 0.2-0.6 g of weight) which provide seedlings with additional reserves (ARÉVALO *et al.* 2007), although this is a temporary benefit. More important on the determination of seedling survival are the distance- or density-dependent factors (JANZEN, 1970; AUGSPURGER, 1984). An escaping pattern was proven for *P. excelsa*, where older seedlings tended to clump significantly further from parent trees because there is probably lower seedling-seedling and parent-seedling competition for resources (ARTEAGA *et al.*, 2006). The role of seed dissemination either by gravity or frugivores dispersal is determinant to escape from the parent tree. Density--dependent factors affecting survival, such as predation or diseases, might be less common in these three species since their contribution to the seedling bank is much lower compared to *L. novocanariensis*.

Acknowledgements

This work has been partially funded by the Rolle foundation and the Programa de Apoyo a la Investigación 2012, from the University of La Laguna. We are grateful to all the field-work collaborators: Eduardo Balguerías, Cristina Blandino, Alistair Domínguez, Gustavo Morales and Priscila Rodríguez.

References

- ALVAREZ-CLARE, S., KITAJIMA, K., 2009. Susceptibility of Tree Seedlings to Biotic and Abiotic Hazards in the Understory of a Moist Tropical Forest in Panama. *Biotropica* **41**: 47-56.
- ANCOCHEA, E., FUSTER, J.M., IBARROLA, E., CENDRERO, A., COELLO, J., HERNÁN, F., CANTAGREL, J.M., JAMOND, C., 1990. Volcanic evolution of the island of Tenerife (Canary Islands) in the light of new K-AR data. *Journal of Volcanology and Geothermal Research* **44**: 231-249.
- ANON., 1973. *Inventario Forestal Nacional. Santa Cruz de Tenerife*. Ministerio de Agricultura (ICONA), Subdirección General de Protección de la Naturaleza, Madrid.
- ARÉVALO J.R., DELGADO J.D., FERNÁNDEZ-PALACIOS, J.M., 2008. Changes in species composition and litter production in response to anthropogenic corridors in the laurel forest of Tenerife (Canary Islands). *Plant Biosystems* **142**: 614-622.

- ARÉVALO J.R., FERNÁNDEZ-PALACIOS J.M., 1998. Treefall gap characteristics and its influence on regeneration in the laurel forest of Tenerife. *Journal of Vegetation Science* **9**: 297-306.
- ARÉVALO J.R., FERNÁNDEZ-PALACIOS J.M., 2000. Seed bank analysis of tree species in two stands of the Tenerife laurel forest (Canary Islands). *Forest Ecology Management* **130**: 177-185.
- ARÉVALO J.R., FERNÁNDEZ-PALACIOS J.M., 2005. Spatial analysis of trees and regeneration of *Laurus azorica* in a laurel forest in Tenerife. *Plant Ecology* **181**: 133-143.
- ARÉVALO J.R., FERNÁNDEZ-PALACIOS, J.M., 2007. Treefall gaps and regeneration composition in the laurel forest of Anaga (Tenerife): a matter of size? *Plant Ecology* **188**: 133-143.
- ARÉVALO, J.R., DELGADO, J.D., FERNÁNDEZ-PALACIOS, J.M., 2011. Regeneration of potential laurel forest under a native canopy and an exotic canopy, Tenerife (Canary Islands). *Forest Systems* **20**: 255-265.
- ARÉVALO, J.R., DELGADO, J.D., FERNÁNDEZ-PALACIOS, J.M., 2007. Variation in fleshy fruit fall composition in an island laurel forest of the Canary Islands. *Acta Oecologica* **32**: 152-160.
- ARÉVALO, J.R., FERNÁNDEZ-PALACIOS, J.M., PALMER, M.W., 1999. Tree regeneration and future dynamics of the laurel forest on Tenerife, Canary Islands. *Journal of Vegetation Science* **10**: 861-868.
- ARÉVALO, J.R., GONZÁLEZ-DELGADO, G., MORA, B., FERNÁNDEZ-PALACIOS, J.M., 2012. Compositional and structural differences in two laurel forest stands (windward and leeward) on Tenerife, Canary Islands. *Journal of Forest Research* **17**: 184-192.
- ARTEAGA, M.A., GONZÁLEZ-DELGADO, G., DELGADO, J.D., FERNÁNDEZ-PALACIOS, J.M., 2006. Offspring spatial patterns in *Picconia excelsa* (Oleaceae) in the Canarian laurel forest. *Flora* **201**: 642-651.
- AUGSPURGER, C.K., 1984. Seedling survival among tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology* **65**: 1705-1712.
- CEBALLOS, L., ORTUÑO, F., 1974. *Vegetación y flora forestal de las Canarias Occidentales*. Cabildo Insular de Tenerife, Santa Cruz de Tenerife.
- CRAWLEY, M.J., 1997. Plant-herbivore dynamics. In Crawley, M.J. (ed.). *Plant Ecology*, pp. 401-474, Blackwell Science, Oxford.
- ERIKSSON, O., 1996. Regional dynamics of plants: a review of evidence for remnant source-sink and metapopulations. *Oikos* **77**: 248-258.
- FERNÁNDEZ-PALACIOS, J.M., ARÉVALO, J.R., 1998. Tree strategies regeneration of the trees in the laurel forest of Anaga. Tenerife. *Plant Ecology* **137**: 21-29.
- FERNÁNDEZ-PALACIOS, J.M., ARÉVALO, J.R., GONZÁLEZ-DELGADO, G., DELGADO, J.D., OTTO, R., 2004. Estrategias de regeneración en la laurisilva. *Makaronesia* **6**: 90-101.
- FERNÁNDEZ-PALACIOS, J.M., DE NASCIMENTO, L., OTTO, R., DELGADO, J.D., GARCÍA DEL REY, E., ARÉVALO, J.R., WHITTAKER, R.J., 2011. A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. *Journal of Biogeography* **38**: 226-246.

- GERHARDT, K., 1996. Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. *Forest Ecology and Management* **92**: 33-48.
- HAMPE, A., ARROYO, J., 2002. Recruitment and regeneration in populations of an endangered South Iberian Tertiary relict tree. *Biological Conservation* **107**: 263-271.
- HUTCHINGS, M.J., 1997. The Structure of Plant Populations. In M.J. Crawley (ed.). *Plant Ecology*, pp. 401-474, Blackwell Science, Oxford.
- JANZEN, D.H., 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* **104**: 501-528.
- KÄMMER, F., 1974. Klima und vegetation auf Tenerife, besonders in Hinblick auf den Nebelniederschlag. *Scripta Geobotanica* **7**: 1-78.
- KAPLAN, E.L., MEIER, P., 1958. Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* **53**: 457-481.
- KITAJIMA, K., 2007. Seed and seedling ecology. In F. Pugnaire and F. Valladares (eds.). *Handbook of functional plant ecology* (second edition), pp. 549-579, Marcel Dekker, New York, New York.
- MAI, D.H., 1989. Development and regional differentiation of the European vegetation during the Tertiary. *Plant Systematics and Evolution* **162**: 79-91.
- MAI, D.H., 1991. Palaeofloristics changes in Europe and the confirmation of the Arctotertiary-Palaeotropical geofloral concept. *Review of Palaeobotany and Palynology* **68**: 29-36.
- MCCUNE, B., MEFFORD, M.J., 1995. *PC-Ord. Multivariate analysis of ecological data, version 2.0*. MjM Software Design, Oregon.
- PARSONS, J.J., 1981. Human influence in the pine and laurel forest of the Canary Islands. *Geographical Review* **71**: 253-271.
- POSTIGO MIJARRA, J.M., BARRÓN, E., GÓMEZ MANZANEQUE, F., MORLA, C., 2009. Floristic changes in the Iberian Peninsula and Balearic Islands. *Journal of Biogeography* **36**: 2025-2043.
- PYKE, D. A., THOMPSON, J.N., 1986. Statistical analysis of survival and removal rate experiments. *Ecology* **67**: 240-245.
- SANTOS, A., 1990. *Bosques de laurisilva en la región macaronésica*. Colección Naturaleza y Medio Ambiente, No. 49, Council of Europe. Strasbourg.
- SILVERTOWN, J.W., 1982. *Introduction To Plant Population Ecology*. Longman, London.
- SPSS, 1986. *SPSS/PC+ V.6.0. Base manual*. SPSS Inc. Chicago.
- WHITMORE, T. C., 1989. Canopy gaps and the two major groups of forest trees. *Ecology* **70**: 536-538.
- WIENS, J.A., 1989. Spatial scaling in ecology. *Functional Ecology* **3**: 385-397.

Entregue para publicação em falta

Aceite para publicação em falta

