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Variation in fleshy fruit fall composition in an island laurel forest of the Canary Islands

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ABSTRACT

Spatial and temporal variations in fruit fall are critical in the structuring of plant populations and are important determinants of canopy composition. We analyzed fruit fall in two laurel forests, near Tenerife, Canary Islands, during one year to quantify temporal variation in fruit abundance and its relationship with canopy composition. There was some temporal synchrony among fruiting tree species in fruit fall phenology at the two study forests. Although the canopy composition of both sites differed significantly, the fruit fall composition did not show significant differences. In spite of that, some species showed differences in abundance between sites, with a greater biomass of *Laurus azorica*, *Ilex perado* and *Myrica faya* at Aguirre than at El Moquinal site. The temporal variation on fruit fall composition was low and it was not possible to infer seasonality in these laurel forests on the basis of fruit fall composition. The analysis revealed significant differences among sites, but not between species.

Our results suggest a potentially important role of frugivores (together with some differences among sites in forest structure) in the spatial fruit pattern. However, temporal patterns are not as clear and only two species showed synchrony in fruit production, which we related with an attenuated seasonality as can be extracted from the lack of differences in fruit production along the different seasons.

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1. Introduction

Spatial and temporal differences in fruit production, fruit fall, and seed distribution are critical in structuring plant populations (Gibson and Wheelwright, 1995; Abrahamson and Laine, 2003), and affect population density and distribution of frugivorous animals (e.g., van Schaik et al., 1993; Curran and Leighton, 2000). Competition between plants, natural regeneration, succession and plant–animal interactions are interconnected processes that depend greatly on the spatial and

temporal patterns of fruit production and deposition (Crawley, 1986). Phenological phenomena, such as reproductive synchrony in forest trees, are often studied over evolutionary and ecological time in a context of interactions with pollinators, seed dispersers and predators (Herrera, 1982; Howe and Smallwood, 1982; Wheelwright, 1985; Stiles and White, 1986; Blake et al., 1990; Clark et al., 2004).

However, phenological patterns of plants are also strongly related to environmental factors (insolation, rainfall, or climatic anomalies), plant endogenous rhythms, competition

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with other plants, and historical and phylogenetical constraints (Herrera, 1995; Fenner, 1998; Bradley et al., 1999; Hamann, 2004). Most studies reporting fruiting phenology in both temperate and tropical forests show a high degree of spatial and temporal variations in the seasonality and phenology of fleshy-fruited trees (Howe, 1984; Hardesty and Parker, 2003).

In our previous work on regeneration in laurel forests, a comparison of seed germination revealed no compositional differences between soil seed banks from contrasting laurel forests, and no relationship between species composition of the soil seed bank and the species composition of the canopy, although high seasonal variability was found in patterns of germination (Arévalo and Fernández-Palacios, 2000). Little is known about the spatial or temporal patterns of fleshy fruit production of tree species in the laurisilva (Valido and Delgado, 1996; Hernández et al., 1999; Delgado, 2002), and there are no studies linking canopy composition, phenology of fleshy fruits through seed rain patterns, and composition of the soil seed bank in the Canarian laurisilva.

The objective of this study, therefore, is to describe temporal variation and spatial patterns of fruiting and the relationships with local canopy species composition in the laurel forest of Tenerife, Canary Islands. We measured seed rain throughout one year in two laurel forest sites to test the following hypothesis: temporal patterns of seed deposition are similar among tree species and fruit fall composition is spatially related to canopy species in both sites. These results will provide useful information on the regeneration ecology of these forests for the subsequent development of management plans and laurel forest restoration in the Canary Islands.

2. Material and methods

2.1. Study site

The study was conducted in the Anaga Rural Park in the northeast corner of Tenerife, Canary Islands (28° 19'N, 16° 34'W). The park encompasses a 7–8 million-year-old basaltic massif (Ancochea et al., 1990) covering ca. 130 km², and represents 7% of Tenerife's total area. We selected two sites in the park among the best-preserved laurel forests of Anaga: El Moquinal (windward slope) and Aguirre (leeward slope). The two sites are ~4.5 kilometers apart. 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 ~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).

In plant community studies in the Canary Islands, it is necessary to account for variability in aspect and wind, as both are important determinants of plant distribution in the island of Tenerife (Fernández-Palacios and de Nicolás, 1995). In this study both sample areas are very close and fruit dispersion by birds is common. This spatial variability should be included

in any design of the experiments with communities in both aspects.

The laurisilva, or laurel forest, is an evergreen, subtropical cloud forest present on the Canary, Madeira and Azores islands. Although subtropical in latitude (27–30°N), the laurisilva resembles the Mediterranean forest of S Europe, but its structure and species composition are closer to some forests in Central Africa, North America and Japan (Santos, 1990; Oshawa, 1999). It has therefore floristic affinities with both tropical and temperate areas. The laurisilva of Tenerife has been extensively exploited since the arrival of Europeans in the 15th century (Parsons, 1981). Today, only 10% of the forest area remains, and it has been formally protected since 1988, currently experiencing little human disturbance. No data are available about the precise forest age, although in 1940s, there was some illegal, small-scale forest exploitation. Air photo interpretation has shown that the extent, physiognomy and canopy cover of the forest has changed little between 1952 and the present.

The canopy height of the Anaga laurel forest is 10–20 m, depending on slope, and canopy cover is 80–90% in mature forest. Maximum canopy heights are found at basin bottoms and decrease progressively towards forest hill ridges. In all, the laurel forest of Anaga contains a total of 19 tree species (Santos, 1990).

There is an important representation of the Lauraceae, with four species in four different genera: *Laurus*, *Ocotea*, *Persea* and *Apollonias*. Dominant species are *Laurus azorica*, *Erica arborea*, *Erica scoparia*, *Ilex canariensis*, *Prunus lusitanica*, *Myrica faya* and *Viburnum tinus*. The dominance of a given tree species depends on site conditions. For example, *E. scoparia* dominates in wind-exposed ridges, *L. azorica* in mesic zones and *E. arborea* in more disturbed areas (Ministerio de Agricultura, Pesca y Alimentación, 1973; Oshawa, 1999). The Aguirre forest (leeward slope) is relatively more diverse than El Moquinal forest (windward slope), and has greater relative abundances of more termophilous tree species such as *Picconia excelsa*, *Visnea mocanera* and *Apollonias barbujana*, as well as of *Persea indica*, and generally a lower abundance of *E. scoparia* and *P. lusitanica*. Nomenclature follows Hansen and Sunding (1985).

There are 15 tree species with bird-dispersed fleshy fruits in the laurel forest (Valido and Delgado, 1996; Table 1), although only 13 were found in this study, all present as adult trees in the studied plots. The main bird frugivores and seed dispersers at our study areas are blackbird *Turdus merula*, European robin *Erithacus rubecula* (seed dispersers) and two endemic fruit pigeons, Bolle's pigeon *Columba bollii* and Laurel pigeon *Columba junoniae* (both acting as dispersers and seed predators; Hernández et al., 1999; Martín et al., 2000; Godoy, 2000; Delgado, 2002). Forest stands and environmental data in the study sites are fully described in Arévalo and Fernández-Palacios (1998, 2003).

2.2. Sampling design

Sample plots were located randomly, using a calculator, a Global Positioning System (GPS) and maps. Between June and September 1999, we established three 50 × 50 m (2500 m²) plots in each of the two study sites. Plots 1–3 were located at El Moquinal and plots 4–6 at Aguirre. Plots at El

Table 1 – Descriptor variables of the study plots in the laurel forest

Variable	El Moquinal 1	El Moquinal 2	El Moquinal 3	Aguirre 1	Aguirre 2	Aguirre 3
Altitude (m)	775	850	820	850	925	810
Aspect	NNE	WNW	NW	SE	S	S
Slope (°)	15	10	30	20	40	30
Understory bush cover (%)	15	20	15	40	60	45
Canopy cover (%)	90	95	95	95	95	95
Bare ground cover (%)	5	10	10	10	5	15
Rock cover (%)	1	5	5	1	10	15
Fleshy-fruit tree species richness	6	5	6	11	10	9

Moquinal were 200–300 m apart, whereas those at Aguirre were 270–750 m apart. In each plot we measured altitude and slope, and estimated canopy cover of the stand using a convex spherical densitometer (Lemmon, 1957). We defined trees as stems of at least 2.5 cm of dbh and calculated basal area and density of the trees. We also visually estimated rock, bare soil cover within each complete plot (Table 1). There is no information about flowering phenology, but the dependence of fruit fall on weather conditions is well known by local people. Our study period was characterised by average values of temperature and precipitation. On this basis, we consider the period to be representative of the general fructification patterns of the laurel forest (Table 2).

Each plot was subdivided by a grid of 25 10 × 10 m subplots. For seed-collecting traps, we used rectangular, black, plastic trays (54 × 40 cm, area 0.216 m², depth 10 cm). Within every plot, we nailed one trap to the ground at all 16 10 × 10 m intersections. This made sample sizes of 16 trays per plot (projected canopy area sampled = 3.456 m²), 48 trays per study site (10.368 m²) and 96 trays in all (20.736 m²). Small slits in the trap bottom allowed drainage. Whole fruits (both ripe and unripe) and seeds were transported to the laboratory in individually labeled plastic bags, counted and identified to species. Traps were checked weekly from October 2000 to November 2001.

The main limitation of our method is that community fruit production was not measured, because an unknown fraction

of fruits that were predated by animals (mainly birds and rats) on the trees was not measured. Instead we are measuring post-dispersal production of the fruit fall that falls by gravity into the traps. Pre-dispersal production varies among species and among months. Moreover, an unknown fraction of fruits felt are probably consumed in, or removed from the traps by animals (mainly rats and invertebrates; Delgado, 2000), but the fraction is not known.

All fruits of the laurel forest canopy species contain one seed, excepting *I. canariensis* and *Ilex perado* which contain 3–5 seeds and *Rhamnus glandulosa*, which contain 3–4 seeds (Table 3 for biometric traits of the fruits). In that case, each four-seed group was considered a complete fruit for analysis. The small, wind-dispersed seeds of the two *Erica* species were not counted in the seed traps as we focused on fleshy fruits. Traps collected fruits and seeds from all fleshy-fruited species present in the plots at the two study sites. The average weight of a random sample of 100 fruits per species was calculated to convert the number of fruits in dry biomass (g/m²).

2.3. Statistical analysis

We tested for differences in mean values of annual fruit production proportions, basal area proportions and tree density proportions between El Moquinal and Aguirre with the Student's *t* test after testing to fulfill parametric assumptions. We also correlated the proportion of basal area of the species

Table 2 – Monthly mean values for temperature and total precipitation in Los Rodeos meteorological station (located near the study site, altitude: 617 m)

Month	1999		2000		2001	
	Precipitation	Temperature	Precipitation	Temperature	Precipitation	Temperature
January	192.8	12.6	90.2	12.4	49.6	13.9
February	12.3	12.4	28.3	14.2	25.3	13.8
March	33.4	13.5	2.2	16.1	39.3	15.1
April	18.2	16.4	38.1	14.5	29.7	15.2
May	0.8	17.0	15.9	16.6	2.7	16.7
June	0.0	18.1	3.5	18.7	0.5	18.9
July	3.9	20.0	6.2	19.9	5.4	20.0
August	8.5	22.1	1.0	21.2	1.7	22.2
September	4.1	20.3	9.8	20.2	14.4	21.0
October	132.7	18.2	38.1	18.5	26.9	20.3
November	103.3	16.7	8.5	15.8	116.6	16.1
December	60.0	13.8	99.1	15.3	50.9	15.8
Total annual for precipitation (mm) and average for temperature (°C)	570.0	16.8	340.9	17.0	363.0	17.4

Table 3 – The most common fleshy-fruited tree species of the laurel forest with relevant fruit and seed traits

Tree species	Family	Fruit length (mm)	Fruit diameter (mm)	Fruit fresh weight (g)	Seed diameter (mm)	Seed weight (g)	No. seeds per fruit	Fruit type	Dispersal mode
<i>Apollonia barbujana</i>	Lauraceae	18.07 (1.97)	13.60 (1.41)	0.85 (0.34)	10.41 (1.39)	0.51 (0.31)	1	Berry	Birds
<i>Heberdenia excelsa</i>	Myrsinaceae	8.19 (1.2)	10.79 (0.5)	0.15 (0.0)	7.16 (0.5)	0.1 (0.0)	1	Berry	Birds
<i>Ilex canariensis</i>	Aquifoliaceae	- ^a	10.44 (0.95)	0.26 (0.08)	3.47 (0.56)	0.03 (0.01)	3-4 ^b -5	Drupe	Birds
<i>Ilex perado</i>	Aquifoliaceae	- ^a	10.63 (1.1)	0.62 (0.2)	3.69 (0.4)	0.06 (0.0)	3-4 ^b -5	Drupe	Birds
<i>Laurus azorica</i>	Lauraceae	16.09 (1.22)	12.16 (0.74)	1.54 (0.19)	10.22 (0.67)	0.84 (0.13)	1	Berry	Birds
<i>Myrica faya</i>	Myricaceae	- ^a	7.76 (1.1)	0.25 (0.1)	4.69 (0.3)	0.04 (0.0)	1	Drupe	Birds
<i>Ocotea foetens</i>	Lauraceae	21.11 (2.19)	14.52 (1.39)	0.72 (0.22)	11.37 (1.36)	0.38 (0.18)	1	Berry	Birds
<i>Persea indica</i>	Lauraceae	18.60 (1.49)	12.71 (0.18)	1.84 (0.15)	10.74 (0.37)	1.16 (0.08)	1	Berry	Birds
<i>Picconia excelsa</i>	Oleaceae	18.91 (1.37)	12.41 (1.05)	0.66 (0.13)	8.74 (0.78)	0.33 (0.07)	1	Drupe	Birds
<i>Prunus lusitanica</i>	Rosaceae	11.57 (1.01)	11.10 (0.78)	0.17 (0.05)	5.75 (0.21)	0.05 (0.0)	1	Drupe	Birds
<i>Rhamnus glandulosa</i>	Rhamnaceae	8.63 (0.74)	8.70 (0.75)	0.13 (0.03)	4.56 (0.58)	0.03 (0.01)	3 ^b -4	Drupe	Birds
<i>Viburnum tinus</i>	Caprifoliaceae	8.73 (0.78)	5.27 (0.42)	0.13 (0.02)	4.47 (0.42)	0.07 (0.01)	1	Drupe	Birds
<i>Visnea mocanera</i>	Theaceae	10.43 (1.36)	8.81 (0.51)	0.21 (0.04)	- ^c	- ^c	1	Fleshy capsule	Birds

Data sources: Juan D. Delgado. Unpublished; Delgado (2000, 2002); Nadine Bauer. pers. comm. Shown are means and standard deviation (in parentheses).

^a For *Ilex* spp. and *M. faya* only fruit diameter was measured as the fruit is roughly spherical.

^b Most common seed number.

^c Very small seeds.

on each plot with the proportion of the species fruit fall (in dry biomass) for both sites.

We used a two-factor analysis of variance to determine the effect of site and species in the amount of fruit biomass collected per month. The month was used as covariate.

Ordination techniques help to explain community variation (Gauch, 1982), and they can be used to evaluate trends in species composition through time and space (ter Braak and Šmilauer, 1998). We applied Detrended Correspondence Analysis (DCA, using CANOCO, ter Braak and Šmilauer, 1998) to examine species composition of the seed rain in each month and plot (three plots per site). Analyses were performed on fruit dry biomass per square meter. We also used DCA to examine species composition of fleshy-fruited trees in the plots at both study sites in terms of basal area per hectare. The plot coordinates from the DCA based on species composition in the seed traps and basal area were analyzed with a logistic regression, with study site as a binary variable (El Moquinal or Aguirre, using Moquinal as 1 and Aguirre as 0), to evaluate the relationship between seed rain composition and tree species composition.

Although the “site” (El Moquinal vs. Aguirre) is obviously not a response variable, it can be used to represent two groups, and can therefore be treated as a dependent variable. Membership of the two groups can be predicted using logistic regression. Whether the two groups differ – in this case as defined by their scores on Axis 1 of the DCA ordinations – can be tested using the Wald statistic (Agresti, 1996).

For all analyses, the significance level was set at $p = 0.05$. Basic statistical methods followed Zar (1996) and were implemented with the SPSS statistical package (SPSS, 1986).

3. Results

We collected a total of 7864 fruits in El Moquinal and 14,458 fruits in Aguirre between October 2000 and November 2001. Fruits and seeds of the following 13 tree species were collected: *A. barbujana*, *Heberdenia excelsa*, *I. canariensis*, *I. perado*, *L. azorica*, *M. faya*, *Ocotea foetens*, *P. indica*, *P. excelsa*, *P. lusitanica*, *R. glandulosa*, *V. tinus* and *V. mocanera*. Mean monthly intensity of fruit fall (dry biomass) was 14.71 g m^{-2} (± 5.92 SD) in Aguirre and 12.5 g m^{-2} (± 3.31 SD) in El Moquinal. Monthly average biomass collected per fruit species followed different patterns at the three plots and both sites. *A. barbujana* and *V. tinus* peaked synchronously at the two sites. *M. faya* (July–September), *P. lusitanica* (June–August) and *P. excelsa* (July–August) produced the bulk of the crop during the summer months (Fig. 1). However, *M. faya* also showed another clear, distinct fruiting peak in winter months. *I. canariensis* and *R. glandulosa* showed a fruiting peak in spring (April–May and May–June, respectively) (Fig. 1). Trees with a local maximum fruiting in autumn–winter were *I. perado*, *O. foetens*, *L. azorica* and *P. indica* (Fig. 1).

Overall fruit production (dry biomass) was dominated by *M. faya*, *V. tinus* and *I. canariensis* in El Moquinal (17.24, 14.67, and 14.70 $\text{g m}^{-2} \text{y}^{-1}$ on average, respectively), and by *L. azorica*, *M. faya* and *I. perado* in Aguirre (23.67, 23.29 and 18.80 $\text{g m}^{-2} \text{y}^{-1}$). Annual fruit production was significantly higher in Aguirre than in El Moquinal for *L. azorica* ($t = 6.54$,

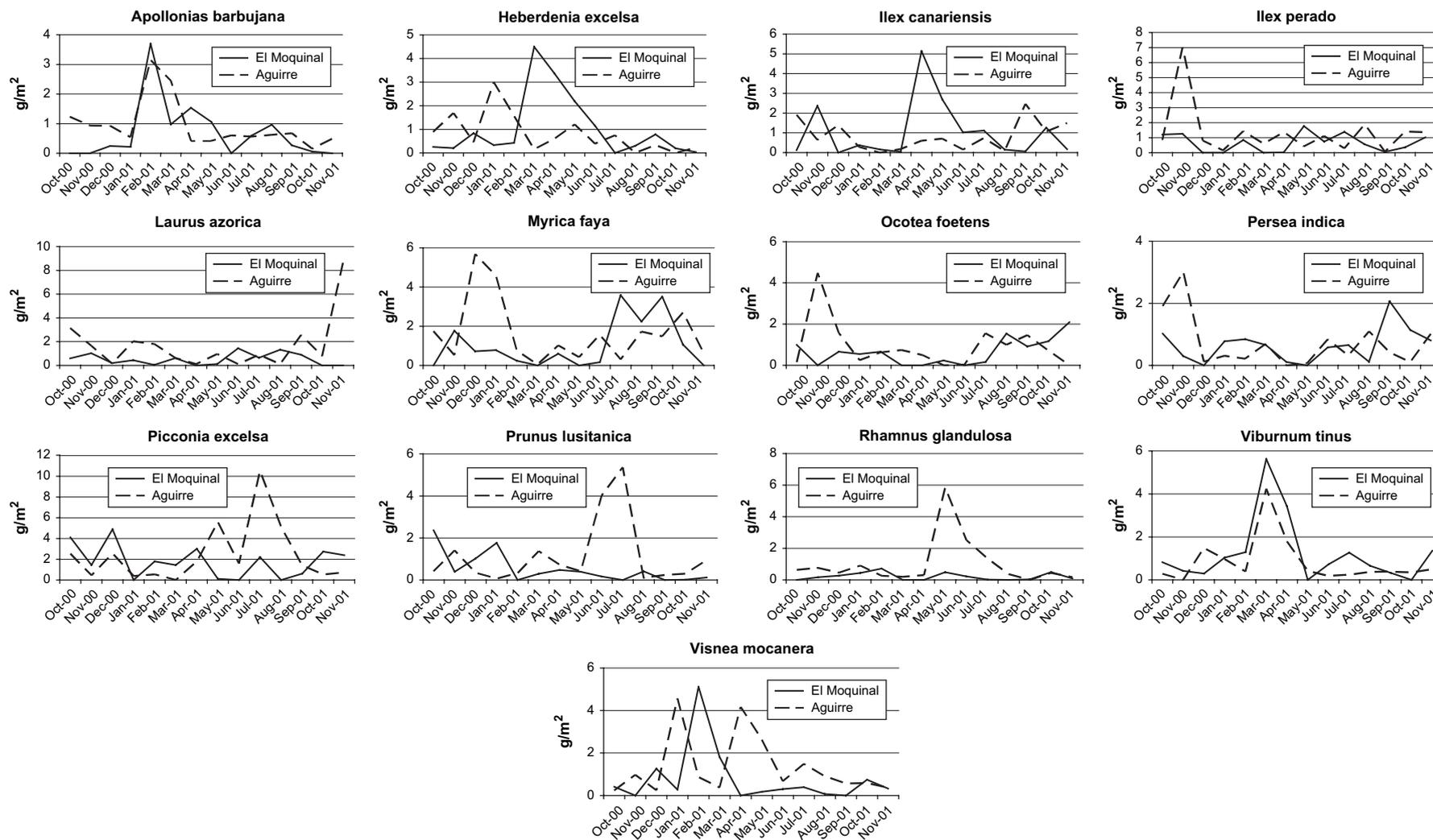


Fig. 1 - Monthly average ($n = 42$) fleshy dry biomass production for the 13 species collected in the fruits traps. For all the species, the collection of fruits started the first week of October 2000 and finished the last week of November 2001.

$p < 0.01$), *M. faya* ($t = 4.60$, $p < 0.01$) and *I. perado* ($t = 4.66$, $p < 0.01$). Annual fruit production for all the species pooled was higher in Aguirre than in Moquinal ($t = 6.813$, $p < 0.01$). Correlation coefficients for each plot relating the proportion of basal area to the proportion of fruit fall were not significant at any of the plots for each site, revealing a low relationship between canopy and fruit fall composition. Basal area ($t = 2.025$, $p > 0.05$) and density of trees ($t = 1.991$, $p > 0.05$) did not show significant differences between the two study sites (Table 4).

However, although the analysis of variance revealed that monthly fruit biomass collected did not differ significantly between species (species: $F = 0.710$, $df = 12$, $p > 0.05$), differences were important between both sites (site: $F = 8.475$, $df = 1$, $p < 0.01$). The interaction between sites and species was not significant.

Results of the DCA based on fruit dry biomass data revealed a poor discrimination in terms of different seasons or sites (Figs. 2 and 3). The logistic regression and Wald test relating the plot scores of the first DCA axis to site was not significant. This indicates that the coordinates of the first DCA axis cannot be discriminated as a function of site ($B = -0.03$, Wald statistic = 0.00016, $p > 0.05$).

We found canopy composition did differ among groups, as measured by basal area and thus, there was good discrimination between the two sites along the first DCA axis (Fig. 4). El Moquinal (the windward site) was dominated by two species, *P. lusitanica* and *I. canariensis*, whereas Aguirre (the leeward site) showed a more diverse array of species (*L. azorica*, *I. canariensis*, *A. barbujana*, *R. glandulosa*, *O. foetens*, *H. excelsa*, *P. excelsa*). The logistic regression relating plot DCA coordinates and sites (El Moquinal-Aguirre) yielded a significant model ($B = -3.112$, Wald statistic = 1.15515, $p < 0.05$).

4. Discussion

Climatic regime in Canary Islands can be considered to be Mediterranean and some subtropical influences. Basically,

Canary Islands has an attenuated Mediterranean climate (Marzol, 2000) in contrast with other continental Mediterranean areas, that are strongly seasonal, with cool wet winters and hot dry summers (e.g., see Herrera, 1995). Compared to temperate forests, subtropical forests experience less intense seasonality, causing high asynchrony in flowering and fruiting phenology across species (Herrera, 1995; Wheelwright, 1988, 2000). The laurel forest is climatically more stable and mild than other Canarian ecosystems, such as the pine forest (Höllermann, 2000). Also, the leeward site in our fruit survey was more productive and diverse, probably due to its southern aspect. The impact of human activities in these forest stands (litter removal and wood extraction) was particularly intense 50 years ago (Arévalo and Fernández-Palacios, 1998), but it has been similar in both study areas. Thus, we could not attribute changes in fruit fall patterns at the two sites to differences in anthropogenic disturbance of the vegetation. Also, forest structure is different at both sites (Table 4), being an important factor determining fruit fall. No data are available about the age of the forest, but it is considered to be a few generations old (Arévalo et al., 1999). Due to that, both study sites are similar with respect to age and disturbance regime.

The analysis of the fruit fall resulted in a poor discrimination of fruit composition between seasons (Fig. 2), although a slight gradient was observed from winter to summer. Canopy composition clearly differed between forest sites, but there was no similar contrasting pattern in fruit fall composition between them (compare Figs. 3 and 4).

We found a higher fruit production in Aguirre than in Moquinal. Because Aguirre is leeward oriented with a warm southern aspect, humidity and precipitation are lower. Consequently, shade intolerant species are more abundant than shade tolerant, as is the case for *M. faya*. These environmental differences can be related to differences in total fruit fall biomass. However, movements of frugivores could attenuate these differences by relocating fruits and thus facilitating a more homogeneous fruit distribution that shows more weak relationships with canopy fruit species composition. We found three species (*M. faya*, *P. excelsa* and *P. lusitanica*)

Table 4 – Basal area (m²/ha) and density (no. of trees/ha) of fleshy-fruited trees at the two study sites

	El Moquinal 1		El Moquinal 2		El Moquinal 3		Aguirre 1		Aguirre 2		Aguirre 3	
	Basal area	Density	Basal area	Density	Basal area	Density	Basal area	Density	Basal area	Density	Basal area	Density
<i>Apollonias barbujana</i>	–	–	–	–	–	–	1.09	116	–	–	1.83	108
<i>Heberdenia excelsa</i>	–	–	–	–	–	–	3.35	332	14.38	632	0.02	8
<i>Ilex canariensis</i>	5.60	1228	10.34	1256	7.58	1060	3.38	496	3.83	308	4.93	444
<i>Ilex perado</i>	1.98	108	–	–	0.72	36	–	–	–	–	–	–
<i>Laurus azorica</i>	7.16	1228	5.43	832	3.82	456	7.96	628	8.13	792	8.67	1028
<i>Myrica faya</i>	5.21	108	2.70	92	2.64	52	9.49	276	5.41	144	10.77	280
<i>Ocotea foetens</i>	–	–	–	–	–	–	–	–	0.01	4	–	–
<i>Persea indica</i>	–	–	–	–	–	–	0.08	4	0.08	4	0.69	32
<i>Picconia excelsa</i>	–	–	–	–	–	–	0.54	12	1.93	20	0.01	8
<i>Prunus lusitanica</i>	13.72	1836	11.81	1504	8.43	728	2.75	140	7.60	700	–	–
<i>Rhamnus glandulosa</i>	–	–	–	–	–	–	1.01	36	1.62	40	0.99	32
<i>Viburnum tinus</i>	0.14	96	0.16	112	0.84	88	0.27	148	1.51	240	0.43	200
<i>Visnea mocanera</i>	–	–	–	–	–	–	0.24	32	–	–	–	–
Total per plot	33.81	4604	30.44	3796	24.03	2420	30.16	2220	44.5	2884	28.34	2140

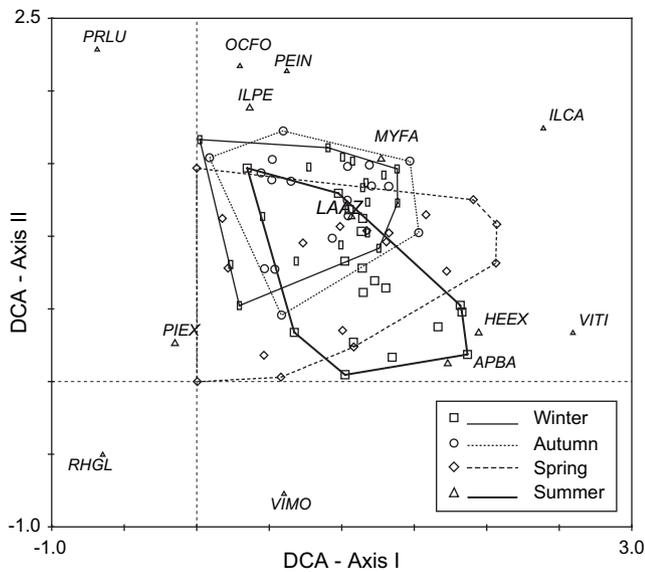


Fig. 2 – Species and plot scores (six plots each month per year, giving a total of 72 plot scores) in the space defined by axes I and II of the DCA based on fleshy dry biomass. Polygons enclose all the plots of the same season: squares are symbols for winter plots (broad solid line), rectangles for summer (narrow solid line), circles for autumn (dotted line) and rhombus for spring plots (dashed line). (Eigenvalues of axes I and II were 0.261 and 0.217, respectively, and the cumulative percentage of variance explained by both axis was 27.4%). (Triangles are symbol for the species). Acronyms – APBA: *Apollonia barbujana*; HEEX: *Heberdenia excelsa*; ILCA: *Ilex canariensis*; ILPE: *Ilex perado*; LAAZ: *Laurus azorica*; MYFA: *Myrica faya*; OCFO: *Ocotea foetens*; PEIN: *Persea indica*; PIEX: *Picconia excelsa*; PRLU: *Prunus lusitanica*; RHGL: *Rhamnus glandulosa*; VITI: *Viburnum tinus*; VIMO: *Visnea mocanera*.

with summer peaks of fruit production, thus making them an important potential source of nutrients for the frugivore community. It may imply that at least the seeds of these tree species may have been preferentially dispersed in summer. This could be an important mechanism of reducing among-species competition among bird dispersers as hypothesized for tropical forest ecosystems (Wheelwright, 1986, 2000).

Analyses of monthly fruit production revealed significant differences among sites but not between species, indicating a general trend of fruit fall that is maximized during winter and spring for almost all the species.

A decrease in overall fruit production was detected in the laurel forest during the summer (Fig. 1), but fleshy fruit production was not entirely discontinuous as is the case in temperate mainland areas (Martín et al., 2000). These results indicate that the laurel forest is comparable in fruit production timing to tropical rain and cloud forests (Wheelwright, 1985, 1988) in spite of its Mediterranean character. In other studies in the Canarian laurel forest, fruit production has been found to decrease during summer months for at least the dominant fruiting tree species (Martín et al., 2000).

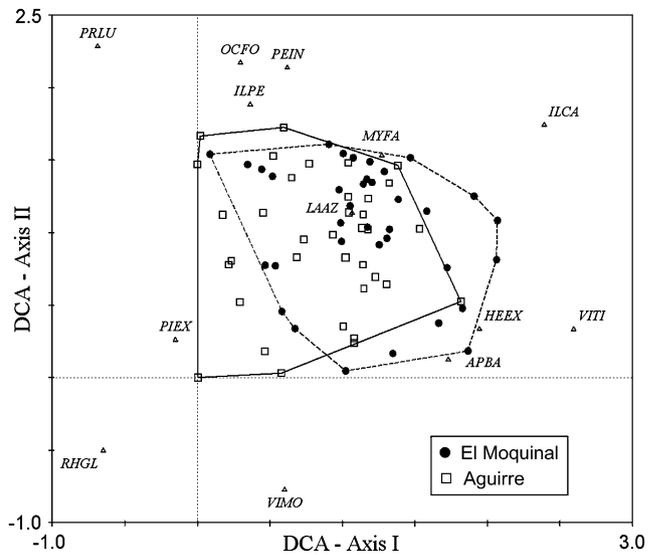


Fig. 3 – Same analysis as Fig. 1, but here polygons enclose all the plots of the same site (El Moquinal, squares symbols and solid line or Aguirre, solid circles and dashed line). Species coordinates are denoted with triangles).

Our results of a weak relationship between canopy composition and fruit fall composition pattern in the laurel forest suggest a potentially important role of frugivores in the dispersal of fruit species beyond the local sites (although

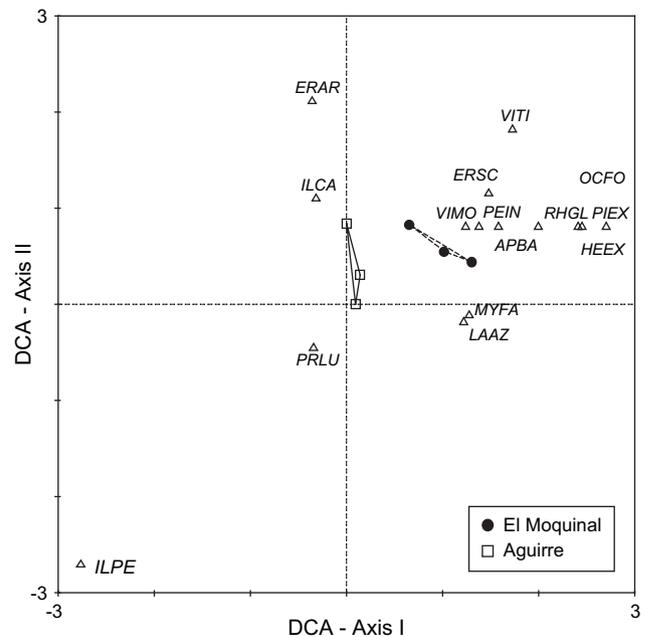


Fig. 4 – Species and plot scores (three plots for El Moquinal and three for Aguirre) in the space defined by axes I and II of the DCA based on basal area. Polygons join the plots of the same site (circles denotes El Moquinal site and square Aguirre site, while triangles the species). (Eigenvalues of axes I and II were 0.268 and 0.044, respectively, and the cumulative percentage of variance explained by both axes was 47.8%). Acronyms – ERAR: *Erica arborea*; ERSC: *Erica scoparia* (the rest of the species, the same as in Fig. 2).

differences in forest structure can also be important together with climate variability per year). The evidence for this is the lack of *I. perado* in Aguirre while present in the fruit rain. A long-term evaluation of fruit production is needed to account for interannual fluctuations, which are probably an important factor leading to variation in fruit production in the laurel forest, along with the detailed spatial patterns in fruit production and use by frugivores.

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