

Floristic and structural recovery of a laurel forest community after clear-cutting: A 60 years chronosequence on La Palma (Canary Islands)

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(Received 19 June 2006; accepted 31 August 2006)

Abstract – We analyzed a post-clearcut chronosequence (0.5 to 60 years after harvesting) in the laurel forest of La Palma island (Canarian Archipelago) to determine the recovery of the stands with respect to species composition, richness, life strategies and structural parameters of the canopy. Multivariate analysis showed that exotic species, as well as annual ruderal species were confined to early-successional stages, while native perennials, typical of laurel forests, dominated the late-successional stages. Total species richness decreased significantly with time after clear-cutting. The relative fast recovery of understory native species may be due to low forest floor disturbance during harvesting. Shade-intolerant pioneer, pioneer-remnant and shade-tolerant late-successional species were the main life strategies of native tree species. Most structural parameters showed a continuous and monotonic increase (basal area, biomass) or decrease (density, percentage of photosynthetic biomass) during succession. Once clear-cutting, here performed with an interval of 8 years, is abandoned, the recovery of the laurel forest seems possible due to careful logging that protects the soil and a rapid asexual regeneration of native tree species, revealing this to be a sustainable management practice.

forest management / laurel forest / species composition / structure / secondary succession

Résumé – Reconstitution floristique et structurale d'une forêt de lauracées après coupe rase : une chronoséquence de 60 ans à La Palma (Îles Canaries). On a analysé une chronoséquence après coupe rase (0,5 à 60 ans après récolte) dans la forêt de lauracées de l'île de Palma (Archipel des Canaries) pour déterminer la reconstitution des peuplements pour ce qui concerne la composition spécifique, la richesse et les paramètres structuraux de la canopée. Une analyse multivariable a montré que les espèces exotiques aussi bien que les espèces rudérales étaient confinées aux premiers stades de la succession, tandis que les espèces naturelles pérennes typiques de la forêt de lauracées dominaient les derniers stades de la succession. La richesse spécifique totale a diminué significativement avec le temps après la coupe rase. La reconstitution relativement rapide des espèces naturelles du sous-bois peut être due à la faible perturbation de la surface du sol forestier au moment de la coupe rase. Les pionnières intolérantes à l'ombre, les pionnières rémanentes et les tolérantes à l'ombre des stades finaux de la succession constituaient les principales stratégies des espèces naturelles d'arbres. La plus grande partie des paramètres structuraux ont montré un accroissement continu et monotone (surface terrière, biomasse) ou décroissant (densité, pourcentage de la biomasse photosynthétique) pendant la succession. Autrefois réalisée ici avec un intervalle de 8 ans la coupe rase est abandonnée, la reconstitution de la forêt de lauracées semble possible grâce à une exploitation prudente des bois protégeant le sol et une régénération asexuée des espèces naturelles d'arbres, révélant que ceci est une pratique de gestion durable.

aménagement forestier / forêt de lauracées / composition spécifique / structure / succession secondaire

1. INTRODUCTION

Sustainable forest management is essential to the establishment and maintenance of a society using resources, products and energy [23]. The impact of harvesting on forest structure and biodiversity is a topic of continuous debate [16, 19, 39]. Government agency regulation determines what, where and when timber is harvested in a managed forest, indicating in some cases which species can be cut [26, 32]. In order to achieve the goal of sustainable forest and illuminate the debate about harvest impacts, the complex natural forest dynam-

ics and vegetation recovery after anthropic harvesting should be studied [44].

The harvesting method with greatest potential impact may be clear-cutting [27, 51]. After clear-cutting, the flora is generally dominated by early successional species and this has been reported to delay the floristic recovery of subtropical forests after clear-cutting [31]. Some late successional plant species may become locally extinct, if cutting is very frequent [27]. In contrast, early-successional species can become rare due to seed bank depletion, if natural disturbance regimes are suppressed and cutting intervals are long (>50 y) [42]. In addition, the type and intensity of forest floor disturbance during

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harvest can influence the regeneration of ground-layer vegetation [9, 37].

Furthermore, the presence of exotic species in understory can be related to forest management, as high intensity treatments increase diversity of both native and exotic species [7]. Oceanic islands are especially sensitive to invasion by exotic species, where invaders can seriously alter function and structure of forest ecosystems [8, 30, 55]. Given that the maintenance of species diversity and species composition has become an important goal of forest management [12, 45], more complete knowledge is needed regarding the effects of harvesting treatments on the floristic composition of understory layers, especially for fragile island ecosystems with a high number of endemic species.

The laurel forest is one of the most emblematic communities of the Canarian archipelago. However, its dynamics remains largely unknown, except for studies on seed bank and gap dynamics [3], which revealed different regeneration strategies of the most important tree species with respect to seed bank, sexual and/or asexual reproduction [4, 20, 21]. Nevertheless, the importance of these functional traits has not yet been confirmed in secondary succession after agricultural use or harvesting. A recent study on roadside effects in the laurel forests revealed that many light-demanding ruderal herbaceous species (both native and exotic) did not penetrate the forest further than 5 m from the edge, probably due to the strong gradient of available light [17]. Allelopathic effects from laurel leaf-litter may also explain this [52]. Consequently, it is important to consider anthropogenic effects in the study of the laurel forest dynamics.

Clear-cutting of small areas of laurel forest stands is the dominant silvicultural technique used on La Palma, and the products have several uses in agriculture [10, 24]. Historically, the main laurel forest products have been: (i) charcoal obtained from stems (5–10 cm of diameter) of mainly *Erica arborea* and *Myrica faya* [10], (ii) several agricultural tools from stems 3–10 cm of diameter and 60–300 cm of height and (iii) green litter for compost production (once used as cattle bed where it is mixed with their excrements).

However, in recent years the most demanded laurel-forest product has been the green litter for compost production in banana plantations. Thus, forest workers have requested a reduction of the cutting time from the local environmental authority. Today the cutting interval has decreased from 10 to 7–8 years, which is considered by forest owners and workers to be adequate for economical exploitation of the stand [10].

Regarding the recovery of a stand after a clearcut, there is little information on environmental parameters (light incidence, soil properties), species composition, structural characteristics of the tree stands (basal area, biomass, percentage of photosynthetic biomass, vegetative sprouting), and the exploitation has been conducted by trial and error until present.

Our aims were: (a) to analyze the floristic and structural changes in laurel forest recovery after cessation of clear-cutting using a 60-years chronosequence; (b) to characterize the role and threats of exotic plant species in the successional process; (c) to confirm previously defined regeneration strategies and functional traits of native tree species, and (d) to eval-

uate the actual harvesting method with respect to economical exploitation and sustainability of the laurel-forest on the island.

2. MATERIALS AND METHODS

2.1. Study site

The study was carried out on La Palma, in an area known locally as “Pajonales” (Fig. 1). “Unidad Insular de Medio Ambiente” manages this area, and part of the site is within the protected area “Parque Natural de Cumbre Vieja”. This area has been designated to meet the timber and woody biomass requirements of the local population; different sectors are assigned for harvesting in different years. The mean altitude of the study site is 1100 m (altitudinal range: 200 m) and most slopes face east. The bedrock is volcanic, with an age of 7–20 Ky [14]; the soils have been classified as umbric Andisols [47]. The mean annual precipitation is approximately 960 mm and the mean temperature is 13.6 °C [2].

The area is dominated by secondary laurel forest stands, with *Erica arborea*, *Laurus novocanariensis*, and *Myrica faya* being the most abundant tree species. Other tree species (*Ilex canariensis*, *Persea indica*, *Viburnum tinus*) are present with lesser abundance in the study site. Old-growth laurel forests do not exist in the vicinity and are confined to steeper slopes in the northeastern part of the island. For further information about the vegetation of the area, see [13] and [49]. Nomenclature of vascular plant species followed [28].

2.2. Design of the experiment

Although the chronosequence approach (space-for-time substitution, [40]) has some disadvantages such as possible small differences between the plots with regard to site history, edaphic and microclimatic conditions or availability of propagules [6, 40], it has been proven an adequate method to study secondary succession [15, 22]. Thus, seven areas, all between 0.5 and 3 ha, and with differing times since the last harvest (0.5, 1, 3, 8, 15, 25 and 60 years after harvesting, “YAH”), but with very similar environmental conditions were selected in the study area. The dates of harvest for the different areas were obtained from the insular government “Cabildo Insular de La Palma” and from 11 aerial photographs of different years.

At each site of the chronosequence, three square plots of 25 m² (5 × 5 m) were systematically selected at regular intervals of 20 to 100 m along a transect, according to the size of the site. To avoid border effects or “current” anthropogenic disturbances, plots were placed at least 15 m from the road. On these destructive plots, we harvested following the traditional clearcutting technique of the island, using five-to six-man groups, with knives and “machetes” and cutting all the vegetation almost at ground level. In the absence of any mechanization system, sampling an area for 100 m² takes approximately one day.

We determined density and basal area of all stems over 2.5 cm DBH (diameter at breast height, including all basal sprouts over that measurement), indicating if the trees were dead or alive, as well as mean aerial biomass (we weighed the total above-ground biomass of the tree), density of living trees, mean tree height, number of suckers (defined as stems taller than 1.5 m and less than 2.5 cm DBH), photosynthetic biomass (we weighed all the leaves of all individuals),

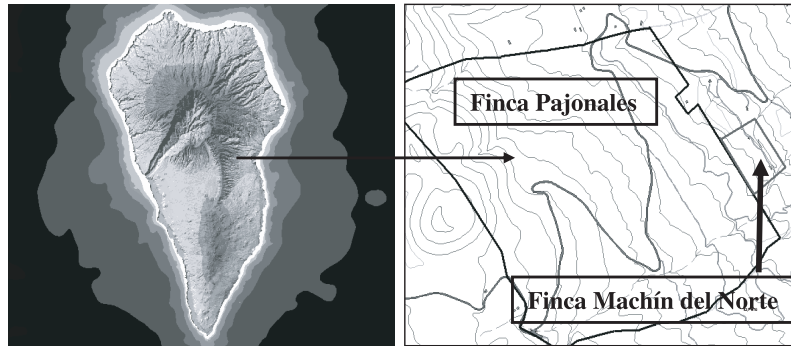


Figure 1. La Palma Island, indicating the location of the study area.

and the regeneration density of tree species (number of seedlings and saplings). We also measured maximum sucker height, density of dead suckers, dead biomass, and calculated the percentage of the photosynthetic biomass in relation to the total above-ground biomass (LMR, leaf mass ratio) [48]. We did not destructively sample the 60-year plots.

In each plot, we collected soil between 0–20 cm below the surface (determined after litter removal) at five random points. We made a single sample of approximately 1 kg for each plot, following the Mascarell et al. [34] method. All the samples were analyzed at “Instituto de Recursos Naturales y Agrobiología de Canarias”. The following parameters were measured for each sample: pH, organic matter (%), Olsen phosphorus (ppm) and exchangeable cations (calcium, sodium, potassium, magnesium extractable in ammonium acetate at pH 7 (ppm)). Finally, we also took litter (dry necromass expressed in kg/m^2) in five 1 m^2 square subplots randomly located within the plot and light incidence (expressed in Klux) at the ground level in all the chronosequence.

We located systematically ten 25 m^2 plots in each site to determine species richness. All the vascular plant species were recorded (see appendix) and some of them collected for identification in the laboratory. These permanent plots will be continuously monitored in future years. Species were classified with regard to introduction status (exotic or native) and life form type (annual, perennial herbaceous, woody), following recently published checklists for the whole archipelago [1, 50] and one for the island of El Hierro [53].

2.3. Statistical analysis

Ordination techniques help to explain community variation [25], and they can be used to evaluate trends through time as well as space [5, 38, 54]. We used Principal Components Analysis (PCA, using CANOCO; [54]) to examine the relationships among the canopy parameters during the chronosequence (weight of green biomass, number of suckers, height of the trees, dead biomass weight, density of live trees, density of dead trees, number of basal sprouts, maximum height of the plot and aerial biomass). We separately applied PCA to relate soil parameters (pH, organic matter, Olsen phosphorus, and extractable changeable cations) to the chronosequence. Since the gradient length of the ordination exceeded 2.5 SD (standard deviations), we decided to use Detrended Correspondence Analysis (DCA; [29]) instead of PCA to examine how species composition changed through the chronosequence. DCA is based on a uni-modal species response to the gradient. DCA analyses were carried out with species pres-

ence data. Non-parametric Kruskal Wallis tests were used to test differences between post-harvest stages within the chronosequence for species richness data and variables of light incidence and litter.

3. RESULTS

Levels of light incidence at ground level (Fig. 2a) changed significantly with time since harvesting ($\chi^2 = 16.4$, $P = 0.012$), dropping dramatically during the three first years after the harvest (YAH), from $2176 \mu\text{mol}/\text{m}^2\text{s}$ 0.5 YAH to less than $50 \mu\text{mol}/\text{m}^2\text{s}$ 3 YAH. Only 15 years after the harvest the light incidence began to recover very slowly, reaching values of ca. $118 \mu\text{mol}/\text{m}^2\text{s}$ (10% of canopy light incidence) at the 60 years plot. Litter accumulation on the soil changed also significantly during succession ($\chi^2 = 15.1$, $P = 0.019$), achieving a minimum of $0.3 \text{ kg}/\text{m}^2$ one YAH and then increasing to 25 YAH (Fig. 2b), where it stabilized at ca. $1.2\text{--}1.3 \text{ kg}$ dry necromass/ m^2 . The amount of litter recorded six months after the harvest (ca. $0.6 \text{ kg}/\text{m}^2$) is very likely the rest of the litter layer of the pre-harvested vegetation.

We found 54 vascular plant species in our plots along the chronosequence (Tab. I). However, only seven have been present in all the ages, the 3 tree species analyzed (*Erica arborea*, *Myrica faya* and *Laurus novocanariensis*), plus 2 ferns (*Asplenium onopteris* and *Pteridium aquilinum*) and two herbs (*Geranium purpureum* and *Pericallis papyracea*). Alternatively, up to 14 plant species have been only recorded in one age of the chronosequence. The mean species richness per age (Fig. 2c), changed significantly with time after abandonment ($\chi^2 = 60.8$, $P < 0.00001$), decreasing from 21 species one year after the harvest to just 5 species (including the 3 studied tree species) 25 years later. Only in the 60 years plot an increment of the species diversity (ca. 10 species) was observed. Mean number of annual and exotic species showed the same temporal trend ($\chi^2 = 62.4$ and $\chi^2 = 52.8$, respectively, both $P < 0.00001$).

Exotic species richness peaked one year after harvesting, when we recorded 5 species per plot (25% of the overall richness), while they were almost absent at the 25 years old stage (Fig. 2c). At the end of the observed chronosequence, only two exotic species persisted in the understory of the closed canopy: the woody species *Ageratina adenophora* and the annual climbing herb *Galium aparine*. During the first three

Table I. List of all vascular plant species found in the chronosequence plots. Abbreviations: P: perennials species; A: annual species; E: endemic species; I: introduced species, N: native species.

Species			Chronosequence plots (years)						
			0,5	1	3	8	15	25	60
<i>Adenocarpus foliolosus</i>	P	E				X			
<i>Ageratina adenophora</i>	P	I	X	X	X	X	X		X
<i>Agrostis castellana</i>	P	I		X					
<i>Aira caryophylla</i>	A	N	X	X	X				
<i>Anagallis arvensis</i>	A	N	X	X	X				
<i>Aphanes microcarpa</i>	A	N	X		X				
<i>Arrhenatherum elatium</i>	P	I	X	X					
<i>Asplenium onopteris</i>	P	N	X	X	X	X	X	X	X
<i>Asterolinon linum-stellatum</i>	A	N	X	X	X				X
<i>Brachypodium sylvaticum</i>	P	N		X					
<i>Briza minor</i>	A	N	X	X					
<i>Calamintha sylvatica</i>	P	N	X						
<i>Carduus clavulatus</i>	A	E	X		X				
<i>Carex divulsa</i>	P	N	X	X					
<i>Cedronella canariensis</i>	P	E	X		X		X	X	
<i>Centaurea melitensis</i>	A	N			X				
<i>Conyza bonariensis</i>	A	I	X	X					
<i>Cistus symphytifolius</i>	P	E			X				
<i>Dryopteris oligodonta</i>	P	E		X		X	X	X	X
<i>Ebingeria elegans</i>	A	N	X						
<i>Erica arborea</i>	P	N	X	X	X	X	X	X	X
<i>Galactites tomentosa</i>	A	I	X	X					
<i>Gallium aparine</i>	A	I	X		X	X	X	X	X
<i>Gallium parisiense</i>	A	N	X	X	X				
<i>Gallium scabrum</i>	P	N	X	X	X	X	X		X
<i>Geranium cf. molle</i>	A	N	X		X				
<i>Geranium purpureum</i>	A	N	X	X	X	X	X	X	X
<i>Gnaphalium luteo-album</i>	A	N			X				
<i>Hypericum grandifolium</i>	P	E	X	X	X	X	X		X
<i>Juncus bufonius</i>	P	N	X						
<i>Laurus novocanariensis</i>	P	N	X	X	X	X	X	X	X
<i>Lotus angustissimus</i>	A	I	X	X					
<i>Mercurialis annua</i>	A	I	X	X			X		
<i>Moehringia pentandra</i>	A	N	X	X	X	X	X		X
<i>Myosotis latifolia</i>	P	N				X	X	X	X
<i>Myrica faya</i>	P	N	X	X	X	X	X	X	X
<i>Neotinea maculata</i>	P	N	X						
<i>Origanum virens</i>	P	N	X	X	X	X			
<i>Ornithopus pinnatus</i>	A	I		X					
<i>Pericallis papyracea</i>	P	E	X	X	X	X	X	X	X
<i>Pteridium aquilinum</i>	P	N	X	X	X	X	X	X	X
<i>Sherardia arvensis</i>	A	N	X	X	X		X		
<i>Sonchus asper</i>	A	I	X		X				
<i>Sonchus oleraceus</i>	A	I	X	X	X				
<i>Tamus edulis</i>	P	N		X			X	X	
<i>Stachys arvensis</i>	A	N	X						
<i>Torilis arvensis</i>	A	N	X	X	X				
<i>Trifolium dubium</i>	A	N	X		X				
<i>Trifolium ligusticum</i>	A	N	X	X					
<i>Tuberaria guttata</i>	A	N	X	X	X				
<i>Urtica morifolia</i>	P	N							X
<i>Vicia grex sativa</i>	A	I		X					
<i>Vicia lutea</i>	A	N		X					
<i>Vicia pubescens</i>	A	N		X					

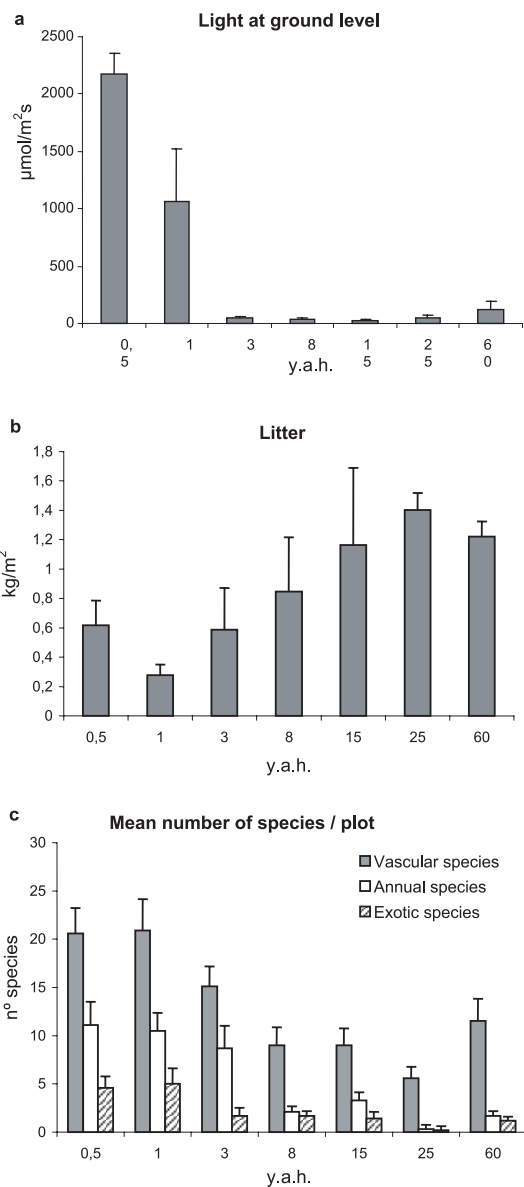


Figure 2. Mean values of chronosequence plot characteristics: (a) Light incidence, (b) litter, (c) vascular plant species richness (total richness, annuals, exotics).

years of abandonment, annuals accounted for more than 50% of the total richness, while in the second phase, once the canopy had closed, woody and perennial herbaceous species dominated the floristic spectrum (Fig. 2c). Fourteen (78%) of the 18 late-successional species, recorded in the last two stages (25–60 YAH), were already present within the first year after clear-cutting.

The three tree species exhibited different patterns of changes in structural parameters along the chronosequence (Fig. 3). The community aerial biomass increased continuously through the chronosequence due to the increase in biomass of *Myrica faya*, while the increase of *Laurus novocanariensis* was less apparent, and *Erica arborea*

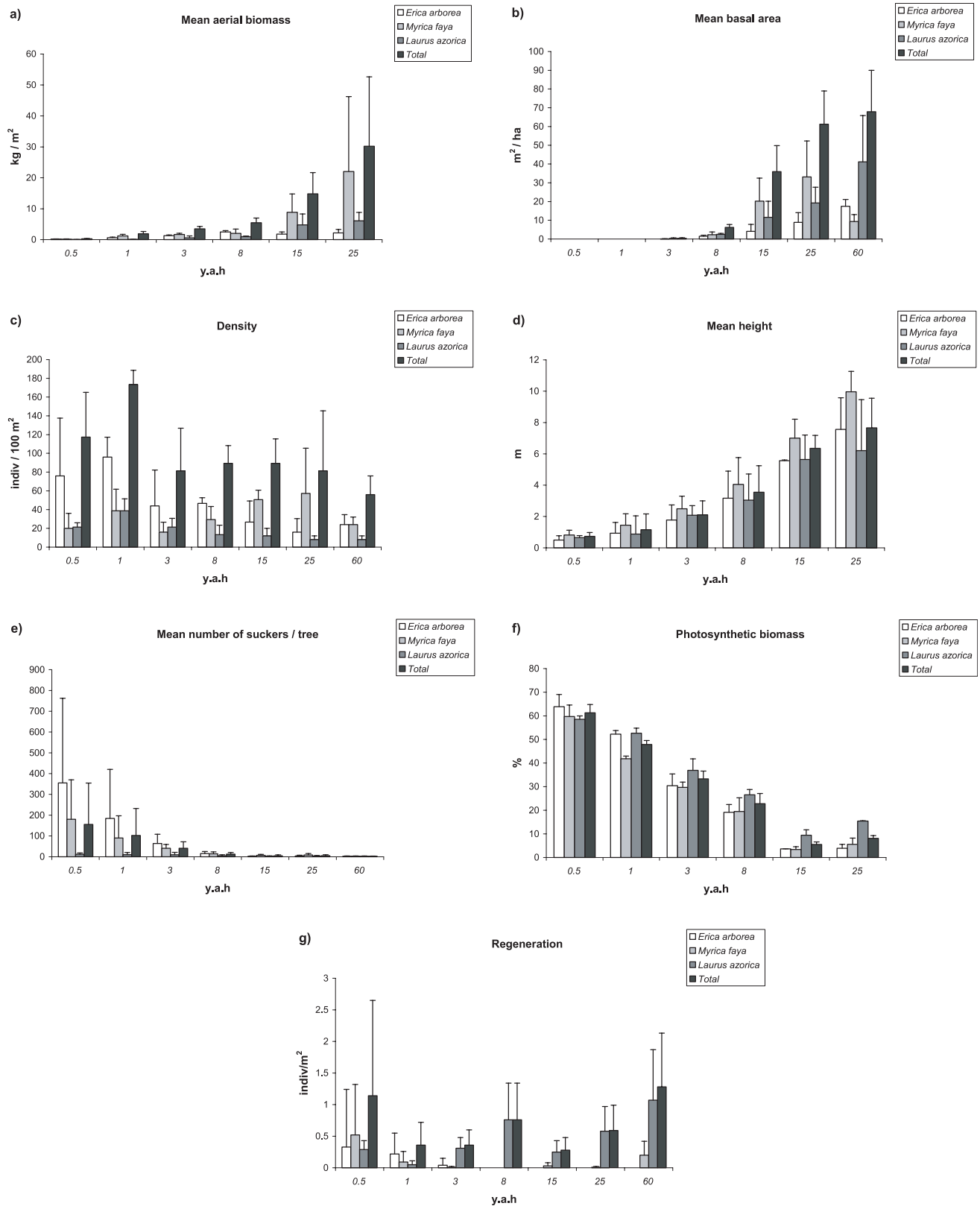


Figure 3. Mean values of chronosequence plot characteristics for different species (*Erica arborea*, *Myrica faya* and *Laurus novocanariensis*) and for the total community. Bars are standard deviation from the mean. (a) Mean aerial biomass; (b) mean basal area; (c) density; (d) mean height; (e) mean number suckers per tree; (f) photosynthetic biomass; (g) regeneration density.

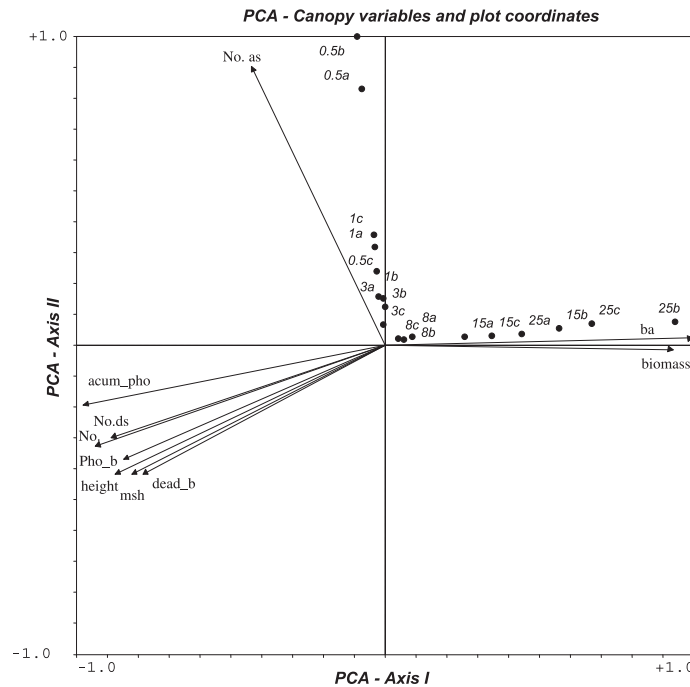


Figure 4. Principal Components Analysis of some of the canopy variables of the plots. Axis I eigenvalue was 0.83 (83% of the cumulative percentage of variance), and axis II eigenvalue was 0.14 (97% of the cumulative percentage of variance). ba: basal area; biomass: total aerial biomass; dead_b: dead biomass; msh: maximum sucker height; height: canopy height; Pho_b: photosynthetic biomass; No.: density of trees; No.ds: density of dead suckers; acum_pho: percentage of photosynthetic biomass; No.as: density of suckers.

decreased 15 years post-harvesting; however, high variability was present along the chronosequence (Fig. 3a). Basal area (analyzed for 60 years) showed a very different pattern. Dominance of *Myrica faya* dropped dramatically after 25 years. *Laurus novocanariensis* became the dominant species with respect to basal area in the 60 YAH sites. Values for the total plot showed some stabilization between 25 and 60 years, with an increase of only $6 \text{ m}^2 \text{ ha}^{-1}$ of basal area in 35 years (Fig. 3b). Tree density decreased for all the species, with *Erica arborea* showing the highest reduction (Fig. 3c). Tree height increased similarly for the three species (approximately 6 m) during the first 25 years (Fig. 3d).

The number of suckers dropped for all species, with the strongest decrease for *Erica arborea* (Fig. 3e). The percentage of photosynthetic biomass (LMR) decreased immediately after harvesting and stabilized after 15 years for all the tree species. Although during the first years after harvesting *Erica* and *Myrica* showed a larger number of suckers per stump than *Laurus*, this species revealed the highest leaf mass ratio at the end of the chronosequence (Fig. 3f), as well as a high basal area (Fig. 3b). This indicates a slower recovery of *Laurus* to the exploitation, and its eventual domination at a very late successional stage.

Although total density of seedlings and saplings did not show clear patterns along the chronosequence (Fig. 3g), regeneration of *Erica arborea* and *Myrica faya* by seedlings and saplings disappeared almost completely after the third year, while *Laurus novocanariensis* maintained similar values along the chronosequence, but with a high variability.

Ordination of the canopy parameters with a PCA revealed that these parameters are useful to discriminate the plots in relation to the time after harvesting (Fig. 4). Early successional stages (0.5 to 3 YAH) are discriminated from one another along Axis 2 on the basis of decreasing number of suckers per stump with increasing stand age, and mid to late successional stages (8 to 25 YAH) are discriminated from one another along Axis 1 on the basis of increasing basal area and aerial biomass and decreasing values of all other structural measures.

The DCA ordination based on species presence was also consistent in discriminating the plots (Fig. 5). Sites 0.5–3 YAH were well discriminated from the rest of the plots by DCA axis I, separating ruderal species (e.g., *Carex divulsa*, *Vicia lutea*, *Arrhenatherum elatium*) dominating during the first three years after harvesting from laurel forest trees (such as *Erica arborea*, *Laurus novocanariensis* and *Myrica faya*) and perennial ferns and herbs (*Asplenium onopteris*, *Dryopteris oligodonta*, *Tamus edulis* or *Myosotis latifolia*), typical of mid to late successional stages (8–60 YAH plots, Fig. 6). Sites 8–60 YAH can be slightly discriminated by axis I but not as clearly as between this site group and the 0.5–3 YAH sites. Plots 3 YAH are discriminated from plots 0.5–1 YAH through axis II.

PCA analysis was not able to discriminate the soil parameters in relation to time after harvesting (Fig. 7), indicating that the soil parameters analyzed are more affected by local substrate heterogeneity than by time after the harvest, being Ca, Na and K contents related to the first axis, and P, organic matter and pH the soil features correlated with the second axis.

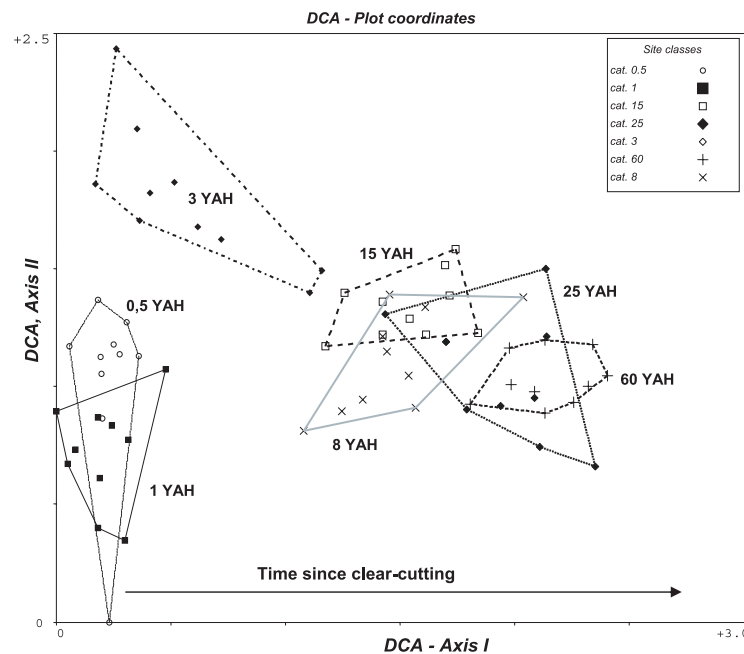


Figure 5. Detrended Correspondence Analysis Axes I and II. Plot coordinates are displayed. Each different chronosequence age has 10 different plots (from “a” to “j”). Envelopes surround 95% of all the plots with the same time after harvesting, covering the minimum possible area. Axis I eigenvalue is 2.40 (cumulative percentage of the variance: 15.58), and axis II eigenvalue was 2.03 (cumulative percentage of the variance: 24.3).

4. DISCUSSION

4.1. Floristic and structural changes

Ordination of species composition showed a clear successional trend coinciding with the recovery of the stand. DCA Axis I separated ruderal species, mostly annuals dominating during the first three years, from woody species highly related with the laurel forest whose importance increased in the second phase of succession. This gradient represents also a replacement of life forms, typical in secondary succession [38, 44]. It has been reported that ruderal annuals and exotic herbaceous plants, most of them light-demanding, are confined to heavily disturbed sites (like roadsides), not being able to grow under a closed laurel forest canopy probably due to competition for light [17]. How far allelopathic effects of litter from laurel leaves prevent those species from establishing inside the forest is topic for future studies [51].

Once the native tree species, all of them already present at the beginning of succession but with a low abundance, have reached to close the canopy, only small changes in species composition after 15 years post-harvesting were observed. These results agree with previous findings that tree fall gaps, the main natural dynamics in the laurel forest, are not expected to change the species composition [4]. Furthermore, they support the succession concept of the initial floristic composition [18], indicating that species have to establish early during succession before competition has increased and resources availability has decreased. In accordance with that, we did not note a delay of floristic recovery due to the dominance of pioneer tree species [31], probably because the pioneer tree *Erica*

arborea was replaced by the late-successional species *Laurus novocanariensis*, already present at the beginning of the secondary succession.

The floristic variation represented by the second DCA axis is more difficult to interpret. The 3 YAH stage is separated by this axis probably due to species such as *Cistus symphytifolius*, *Gnaphalium luteo-album*, *Centaurea melitensis* and *Asterolinum linum-stellatum*, not shared with any other stage. This can rather be related to special site conditions and/or landscape position than to successional trends.

Most of the structural parameters changed considerably with time since harvesting, indicating clearly a structural recovery of the vegetation after the clearcutting, which can be divided into three different stages: (i) the initial stage, between 0 and 1 YAH, showing the highest percentage of photosynthetic biomass and the highest number of suckers in the chronosequence, (ii) the intermediate stage, until 15–25 YAH, with high rates of mortality and selection of suckers being the growth in height more important than the production of new suckers, and (iii) the final stage, after 15–25 years, the forest begins to stabilize.

Soil parameters such as total nitrogen and percentage of organic matter cannot be related with time after harvesting, despite the fact that this relationship has been found in other studies [33]. The increase in output of nutrients due to erosion [11] was not supported by our results, as long as the decrease or increase of nutrients is not related with the chronosequence, suggesting that erosion due to this type of harvesting is not as important as in other forests, what will make shorter the recovery time [43]. In addition, it is important to note that slope values are low for all plots of the study (3–6 sexagesimal degrees).

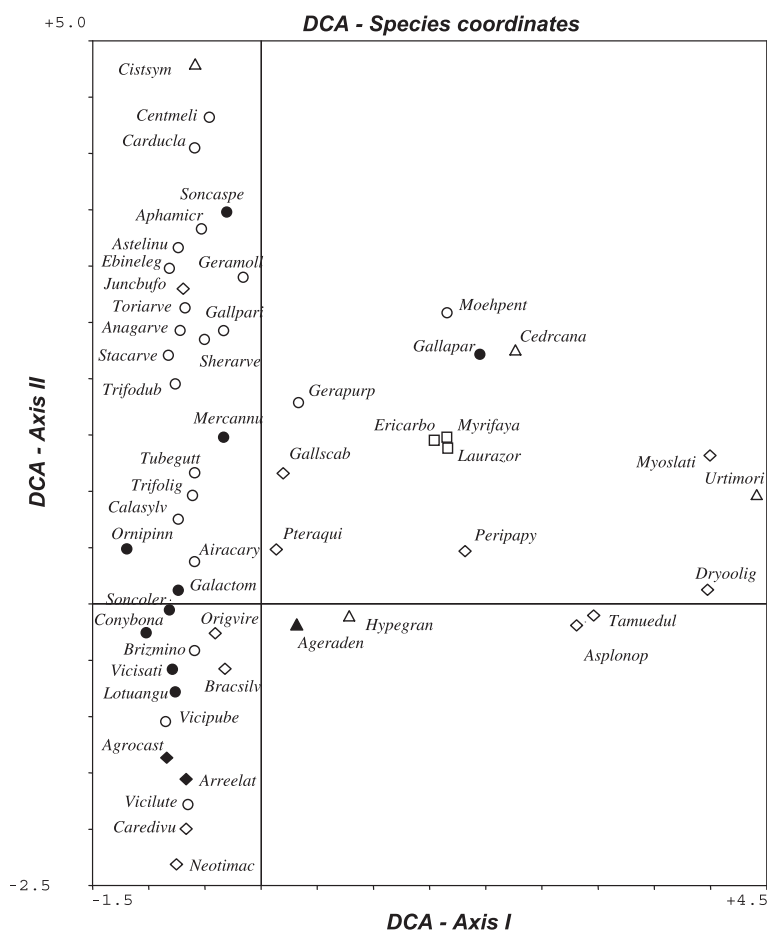


Figure 6. Detrended Correspondence Analysis Axes I and II. Symbol type: circle: annuals; rhombs: perennial herbs; triangles: shrubs; squares: trees; filled symbols = exotic species; open symbols: native species. Species coordinates: *Adenocarpus foliolosus*: Adenfoli; *Ageratina adenophora*: Ageraden; *Agrostis castellana*: Agrocast; *Aira caryophyllaea*: Airacary; *Anagallis arvensis*: Anagarve; *Aphanes microcarpa*: Aphanicr; *Arrhenatherum elatium*: Arrhelat; *Asplenium onopteris*: Asplonop; *Asterolinon linum-stellatum*: Astelino; *Brachypodium sylvaticum*: Bracsylv; *Briza minor*: Brizmino; *Calamintha sylvatica*: Calasylv; *Carduus clavulatus*: Cardclav; *Carex divulsa*: Caredivu; *Cedronella canariensis*: Cedrcana; *Centaurea melitensis*: Centmeli; *Conyza bonariensis*: Conybona; *Cistus symphytifolius*: Cistsymp; *Dryopteris oligodonta*: Dryoolig; *Ebingeria elegans*: Ebineleg; *Erica arborea*: Ericarbo; *Galactites tomentosa*: Galatome; *Gallium aparine*: Gallapar; *Gallium parisiense*: Gallpari; *Gallium scabrum*: Gallscab; *Geranium cf. molle*: Geramoll; *Geranium purpureum*: Gerapurp; *Gnaphalium luteo-album*: Gnaplute; *Hypericum grandifolium*: Hypegran; *Juncus bufonius*: Juncbufo; *Laurus novocanariensis*: Laurazor; *Lotus angustissimus*: Lotuangu; *Mercurialis annua*: Mercuannu; *Moehringia pentandra*: Moehpent; *Myosotis latifolia*: Myoslati; *Myrica faya*: Myrifaya; *Neotinea maculata*: Neotmacu; *Origanum virens*: Origvire; *Ornithopus pinnatus*: Ornipinn; *Pericallis papyracea*: Peripapy; *Pteridium aquilinum*: Pteraqui; *Sherardia arvensis*: Sherarve; *Sonchus asper*: Soncaspe; *Sonchus oleraceus*: Soncoler; *Tamus edulis*: Tamuedul; *Stachys arvensis*: Stacarve; *Torilis arvensis*: Toriarve; *Trifolium dubium*: Trifdubi; *Trifolium ligusticum*: Trifligu; *Tuberaria guttata*: Tubegutt; *Urtica morifolia*: Urtimori; *Vicia grex sativa*: Vicisati; *Vicia lutea*: Vicilute; *Vicia pubescens*: Vicipube.

Minimizing forest floor disturbances favors the natural regeneration and recover of the species composition [37, 46].

4.2. Species richness and exotic species

Total species richness is highest just after clear-cutting (0.5–1 year), which can be attributed as much to the rapid establishment of ruderal species with a high dispersal capacity [42], as to the native species still present in form of seeds or suckers after logging. The rapid closure of the canopy after 3 YAH reduced the number of species, in agreement with

the observed elimination of light-demanding ruderal species. The late increase in richness at the end of the chronosequence could indicate that floristic recovery has not finished and that shade-tolerant native species continue to immigrate slowly due to limited dispersal capacity and/or limited propagule pressure.

Since most of the exotic species were annuals or herbaceous, they were excluded along the chronosequence, and thus occurred at very low abundances at the advanced stages. Although the observed replacement of exotic species by native species seems to be a general trait of secondary succession

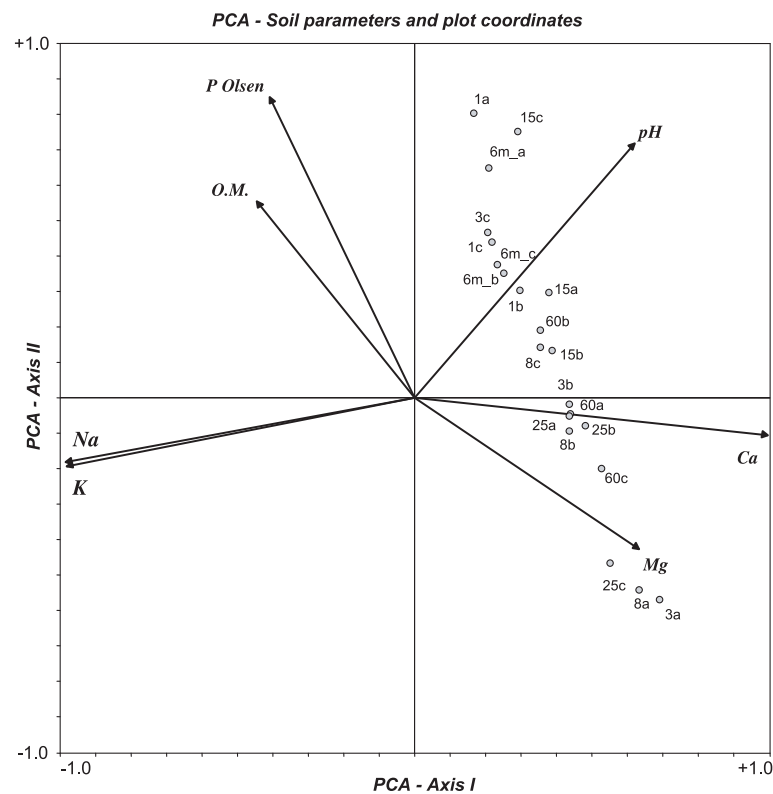


Figure 7. Principal Components Analysis of soil parameters. Axis I eigenvalue was 0.94 (94% of the cumulative percentage of variance), and axis II eigenvalue was 0.03 (97% of the cumulative percentage of variance). P Olsen: Olsen phosphorus; O.M.: organic matter; pH: pH; Na: extractable sodium; K: extractable potassium; Ca: extractable calcium; Mg: extractable magnesium.

related to resource availability, disturbance and life history traits of the invading species [22, 35, 38], it is surprising that, up to now, no exotic tree species is reported to have seriously invaded laurel forest stands on the Canaries, in contrast to other oceanic islands, where invaders caused tremendous impacts on native evergreen forests [8, 30, 55]. The great threat for the Canarian laurel forest could be some shade-tolerant, fast growing colonizer of disturbed sites with high photosynthetic efficiency, good asexual and sexual reproduction, i.e. with combined characteristics of a pioneer and late-successional species. Such a species could be *Pittosporum undulatum*, which has invaded the laurel forests of Madeira and the Azores as well as tropical forest on Jamaica [8].

4.3. Regeneration strategies of tree species

Results show a different successional pattern for each of the tree species. Sexual regeneration after a clear-cut is only possible for pioneer species, possessing seed banks where germination is prevented in close canopies but common on logged areas due to the heliophylic character of their seedlings. This is the case of *Erica*, and to some extent of *Myrica* as well [21], which present seedlings along the chronosequence until the canopy is too closed (> 3 YAH) to receive enough light on the forest floor. Subsequently, only seeds of mature species, such as *Laurus* [21], can germinate under a closed canopy.

Thus, *Laurus* seedlings prevailed in the chronosequence after the first years, and those present in the 0.5–3 YAH plots, are likely survivors of the pre-logged vegetation.

Although often considered a pioneer species, *Myrica faya* has recently been classified as a pioneer-remnant species due to its ability to persist under closed canopies through suckers [21]. After 25 years post harvest, the basal area of *Myrica faya* dropped in favor of *Laurus novocanariensis*, a shade tolerant species. Canopy projection models also predict this pattern for the laurel forest of Tenerife; a higher dominance of *Laurus novocanariensis* is projected in the future even in well-conserved forests [5]. Conditions in 60 YAH sites are likely more favorable for shade-tolerant species. The observed decrease of leaf mass ratio in the first 15 years indicates a shift in biomass allocation from leaves to stems, which is characteristic during forest succession [41].

4.4. Sustainable management practices in the laurel forest of La Palma

After 8 years the structure of the stand is far from the natural structure of the forest; however, at this moment trees typically reach an adequate size for exploitation [10], whereas the community still supplies an important percentage of green biomass and a sufficient number of well-developed suckers, thus matching the necessities of both agricultural tools and

compost precursors. The decrease in photosynthetic biomass and the increase in basal area between 8 and 15 YAH coincide with a reduction in the density and quality of the desired harvestable material.

The species composition of the sites did not show drastic differences among 8–60 YAH sites, which is probably related to the high quality of the soils and the low disturbance of the forest floor during the logging. Furthermore, no invasive species have been detected and no remnant species are favoured by the harvesting, suggesting a high degree of sustainability with this management practices. However, some species (*Viburnum tinus*, *Ilex canariensis*), which are very abundant in similar areas of other islands, as well as on La Palma, show a low abundance in these managed areas. This can be related to the long-term management practices.

In short, results suggest that the current historical management of laurel forest (harvesting with 8 years intervals) does not allow the full structural recovery of the stand. However, although we cannot compare with old-growth stands in this case, species composition seems to recover well and environmental conditions are favorable for the recovery of the stand once these traditional practices are abandoned due to the progressive reduction of demand for these products [36]. Until then, the traditional management of the stand is only meeting the social and economical requirements for part of the population of La Palma.

Acknowledgements: We thank the “Cabildo de La Palma” for the support of the project. Suzanne McAlister and Jerry Husak (Oklahoma State University) revised the manuscript and supplied valuable comments.

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