

Offspring spatial patterns in *Picconia excelsa* (Oleaceae) in the Canarian laurel forest

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Abstract

We studied the spatial patterns of seedlings and seeds in isolated *Picconia excelsa* (Oleaceae) trees in the laurel forest of Anaga, Tenerife (Canary Islands). By finding isolated trees we assessed the correlation of seed and seedling bank traits and parent trees by removing the confounding effects of proximity (< 100 m radius) of conspecific fruiting trees. We counted all the seedlings per age (height) class within its parental range, and sampled the seed number along transects departing from beneath the parent canopy at regular intervals. We mapped all seedlings per age class and plotted seed and seedling profiles in relation to distance to parent trees. Older *Picconia* seedlings tended to clump significantly further from parent trees than younger seedlings, which clumped just beneath the parents. We found significant differences among distances to parent tree in numbers of seedlings per age class. The seedling bank area was significantly correlated with maximum distance of seedlings to parent trees. The majority of seeds were deposited within the first 4 m below the parent crown. Seedlings amount at further distances from the trees is larger than seeds/fruits as counted on the ground. Our results suggest that disseminated, older seedlings have occupied germination sites far from the parent tree because there is probably lower seedling–seedling and parent–seedling competition for resources, and perhaps no intraspecific allelopathy and predation/disease.

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Introduction

Through fruit and seed dispersal, and subsequently seedling recruitment, spatial patterns of seedling establishment and growing to maturity will determine the future configuration and location of forest tree species and thus the community spatial structure (Augspurger,

1983a, b; Condit et al., 1992; Crawley, 1986; Nathan and Muller-Landau, 2000). The spatial distribution of the seedlings of such trees is determined by: (i) the distribution of parent trees producing seeds; (ii) the seed rain pattern around parent trees; (iii) the abundance and effects of seed and fruit dispersers and predators; and (iv) the spatial distribution of suitable germination microsites (Connell, 1979; Janzen, 1970; Rabinovitz and Rapp, 1980; Schupp, 1995).

The Canarian laurel forest is the most diverse terrestrial ecosystem of Macaronesia (including the

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volcanic archipelagos of Azores, Madeira, The Canaries and Cape Verde), and shares some relict floristic affinities with tropical forests (Santos, 1990). In comparison with tropical rain forest, the subtropical laurel forest, a relict formation from the Tertiary, is relatively poor in tree species. However, compared to continental forests of the Mediterranean Region, the Canarian laurel forest is rich in tree species. In all, there are approximately 20 palaeoendemic tree species, but in general, the forest canopy is locally formed by some 10 species. Typically, the most abundant species are *Laurus novocanariensis*, *Myrica faya*, *Ilex canariensis* and *Erica arborea* (Arévalo and Fernández-Palacios, 2003).

Up to 15 tree species of the Canary Islands laurel forest produce fleshy fruits that display an endozoochorous (mostly ornithochorous) syndrome. Composition and variability of the seed rain influences the soil seed bank and creates resources for frugivores and seed dispersers in this forest to an unknown extent. Competition between plants, natural regeneration, succession and plant–animal interactions are interconnected processes that depend greatly on the spatial and temporal pattern of fruit production and fruit traits in any forest (Augspurger, 1983a; Barbour et al., 1987).

The biotic and abiotic factors shaping spatial and compositional patterns, and regeneration of trees in the Canarian laurel forest are only partially known (Arévalo and Fernández-Palacios, 2003; Fernández-Palacios and Arévalo, 1998). Research to date on laurel forest structure and dynamics has been focused on ecophysiology (Jiménez et al., 1996; Morales et al., 1997; Tausz et al., 2004), allometric relations (Aboal et al., 2005), spatial patterns, seed bank composition, regeneration and gap dynamics (Arévalo and Fernández-Palacios, 1998, 2000, 2003; Ohsawa et al., 1999). In those forest patches, some frequent tree species show patterns of aggregation over large distances (*Erica*, *Myrica*, *Ilex*) whereas others are aggregated over shorter distances (*Laurus*, *Prunus*) (Arévalo and Fernández-Palacios, 2003). Analysis of juvenile and adult tree distribution is limited by sample size for the scarcer tree species.

An important issue in forest regeneration and dynamics is the relationship between the spatial distribution of seeds and seedlings regarding parent trees. The spatial distribution of parent plants partly reflects the spatial pattern of seedling recruitment (Arrieta and Suárez, 2005, 2006; Schupp, 1995). It was originally postulated for tropical forests that with increasing distance from parent tree the density of deposited seeds decrease and probability of survival increases (Janzen, 1970). The recruitment curve shows a peak at certain distance from the parent tree. Mortality is also assumed to be density-dependent through risk of predation and pathogens (Connell, 1979). Because of

these processes, the distribution of adult trees is less aggregated than the seedling distribution (Crawley, 1986).

To assess the spatial patterns of seed and seedling distribution from a given parent tree species, it is necessary to make sure that these propagules come from a known progenitor plant. One method to achieve that is to find isolated trees of the focal species presenting a seedling bank, considering as seedling bank all the seedlings in a determined areas which are considered to have a similar origin (Silvertown, 1987). Although without carrying out genetic analyses we cannot be completely sure that all the propagules come from the isolated parent tree, we still could assume that the vast majority of the seeds and seedlings come from it. Indeed, a negligible amount of propagules could be transported by bird dispersers and establish as an indistinct individual seedling in the local seedling bank. Such a study has been carried out in the present work with the fleshy-fruited tree *Picconia excelsa* (Aiton) D.C. (Oleaceae). Excepting some patches where *Picconia* is locally abundant, this species is widely spaced and relatively infrequent (compared to other laurel forest tree species). We studied spatial patterns of parents and seedlings and seed shadows in *P. excelsa*, because: (a) it shows a relatively widely spaced distribution; (b) is more probable to find a visible seedling bank with individuals in different growing stages (age structure more evident). Other frequent fleshy-fruited trees of this forest (*Laurus*, *Apollonias*, *Persea* and *Ocotea*), attain a single sized seedling bank (Oscars, *sensu* Silvertown, 1987); once the seed reserves are consumed the seedlings must persist without growing until a canopy gap is formed. Also, *P. excelsa* has a similar spatial pattern as other species of the laurel forest (e.g. *Rhamnus glandulosa*) and results from this species may be extrapolated for trees with similar patterns in seed dispersion.

Here we studied isolated trees of *P. excelsa* (individuals showing non-overlapping seed shadows, more than 100 m away from conspecifics), to analyze the patterns of seed and seedling distribution regarding parent trees without the confounding effects of nearby conspecifics. We evaluated relationships among different parameters of the trees and of the offspring population to know the possible causes of their spatial arrangement. We asked whether the seedling banks from different parent trees share common characteristics in terms of age structure and shape, size or direction of spreading of the seedling bank. In addition, we asked if there is a relationship between distance to the parent tree and seedling age, which would be an indirect indicator of final seedling survival (recruitment). Finally, we wanted to know the degree of overlapping between the seed shadow and the seedling distribution for each parent tree.

Material and methods

Study area

The study was conducted in the Anaga massif, NE Tenerife, covering ca. 150 km² that represents 7% of the total island area (Fig. 1). The geological age is around 7–8 Million years (Ancochea et al., 1990). The climate is humid-Mediterranean and the mean annual temperature is 15 °C with minimal annual and daily fluctuations. The annual precipitation reaches 900 mm, but can be twice this amount if fog drip is included (Kämmer, 1974). Soils have been classified in the order Entisol, suborder Orthens (Fernández-Caldas et al., 1985).

Some palaeo-endemic trees few of them belonging to the Lauraceae (Santos, 1990) form the laurel forest. Some important species of this forest are *L. novocanariensis* Rivas-Mart. et al., *Apollonias barbujana* (Cav.) Bornm., *Ocotea foetens* (Aiton) Baill., *Persea indica* (L.) C.K. Spreng., *P. excelsa* (Aiton) DC (Oleaceae), *Visnea*

mocanera L.f. (Theaceae), *Prunus lusitanica* L. (Rosaceae), *I. canariensis* Poir. (Aquifoliaceae). The species composition varies according to orientation, height over sea level, etc. Canopy height of the laurel forest of Anaga varies between 10 and 20 m, exceptionally 25 m, depending on slope (Arévalo et al., 1999).

Methods

P. excelsa is an endemic tree species of Madeira and The Canaries. It is relatively abundant in sunny and dry areas of the laurel forest, mostly between 850 and 1150 m elevation, although it can be found in moist and shadowed areas too. Its height is variable reaching up to 20 m in wet areas, and lower in dry areas. Ship rats (*Rattus rattus*) predate both leaves and fruits (Bañares and Barquín, 1982), and saplings and seedlings can be completely defoliated by them. Its fruits are 2 cm long fleshy drupes with a single large seed that turn from green when immature to blue when ripe. Fruits have

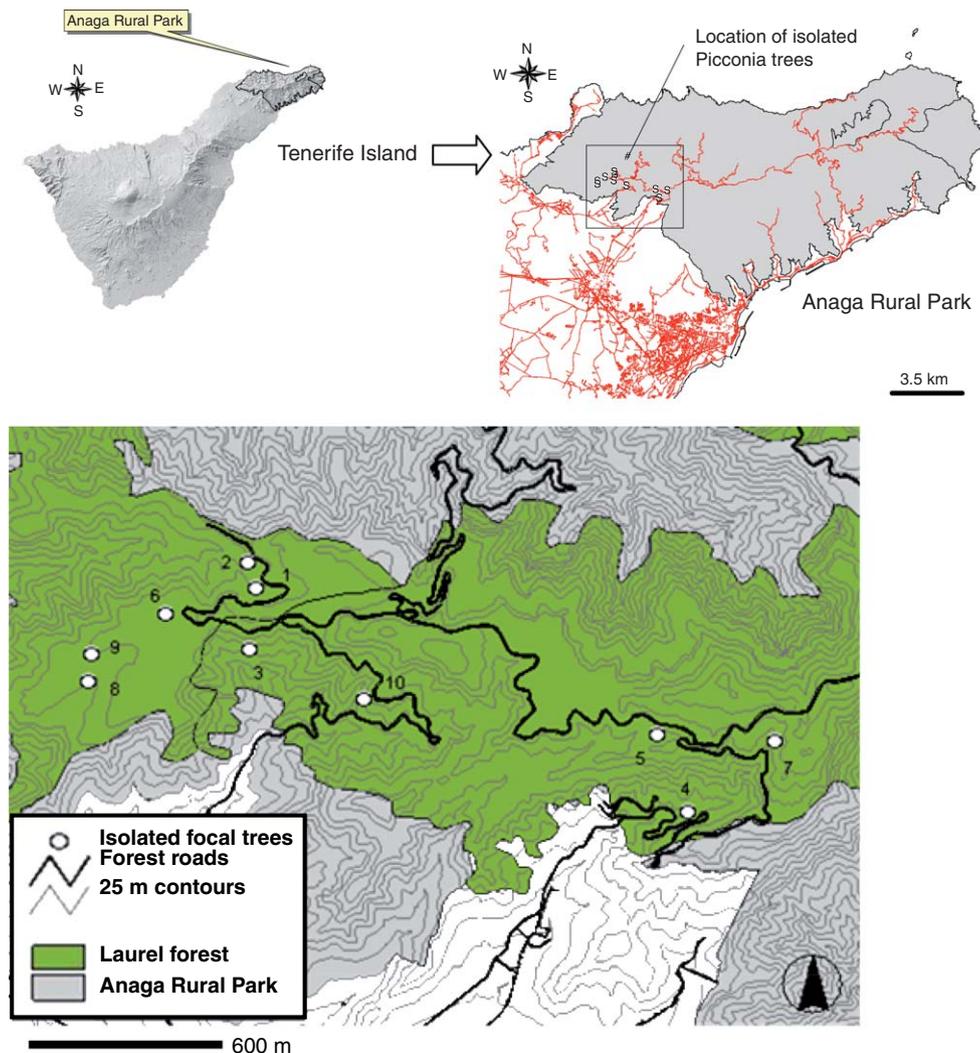


Fig. 1. Map of the study area and location of focal *Picconia excelsa* trees within the laurel forest of Anaga.

1%, 0.7%, 0.35% and 1.22% protein, starch, total sugar and lipid content, respectively (Nadine Bauer, pers. comm.). For further description of this tree, see Bañares and Barquín (1982). *P. excelsa* and other tree species (*L. novocanariensis*, *I. canariensis*, *A. barbujana*) seem to display a mature-itinerant reproductive strategy (Fernández-Palacios et al., 2004), with fleshy fruits dispersed by gravity and by frugivorous birds (mainly *Turdus merula*, *Columba bollii*, *C. junoniae*) (Valido and Delgado, 1996; Delgado and Valido, 1998; Martín et al., 2000). The seedlings germinate mostly at the end of the spring and beginning of the summer, and grow fast to 7–8 cm height keeping both cotyledons up to 1 month after germination. Seedlings experience a high mortality rate (80–85%) (G. González-Delgado, pers. obs.).

The spatial pattern of *P. excelsa* is based on isolated trees, with a high overdispersion, in comparison with other species of the laurel forest. We searched for mature trees of *P. excelsa* fulfilling these requisites: (i) other conspecific mature trees were absent within a 100 m-radial circle; and (ii) fertile trees having their own seedling bank. We scanned for such trees in different stands of the Anaga laurel forest, following our own field experience, and helped by the knowledge of experienced forest guards. We searched for isolated parent trees with an associated seedling bank, and hence we discarded isolated trees without seedling banks or banks with two or more putative parents. This was a chief limitation for the sampling sizes of this work.

When an isolated tree was found, we took abiotic data about aspect, mean slope and altitude of the stand. As biotic data, we recorded diameter of trees at breast height (DBH), height and canopy cover of the parent tree. By using a (*x,y*) coordinate grid, we mapped the position of all the seedlings present and measured their height establishing five size (age) classes: 1: 0–10 cm; 2: 10–20 cm; 3: 20–40 cm; 4: 40–60 cm and 5: 60–100 cm. Saplings over 100 cm were not included. Although this relationship is highly variable, these classes were appropriate, as they were associated with seedling age.

To study the spatial pattern of the seed/fruit rain, we randomly chose one direction forming a straight line with origin at the parent tree. Then we selected three additional lines at a 90° angle with the first line around each tree. Data from the four lines were used to average seed rain per tree. Along each line, we placed 1-m² quadrats every 1 m for fruit counting. Inside each quadrat we counted unripe and ripe fruits and seeds on the ground. Slope and aspect was noted for each fruit counting line. The following seed/seedling bank traits were recorded: total number of seedlings and seeds/fruits, total area of the seedling bank around parent tree, seedling density, mean distance from seedling to parent trees, distance from parent tree to the farthest seedling, mean seedling height, and maximum seedling height.

We used Pearson correlation analysis to study the association between seedling size and distance to parent tree. Differences among distances to parent tree in the number of seedlings per age class were tested with one-way ANOVA (for a $p < 0.05$). We applied multivariate regression to evaluate the independent variables significantly affecting the maximum distance reached by seedlings in respect to parent tree (Zar, 1996).

Results

Characteristics of trees and sizes of fruit and seedling banks

We have been able to detect 10 *Picconia* individuals matching the isolation requirements (# 1–8). Two further isolated trees (# 9 and 10) completely lacked fruit and seedling bank, and thus were not included in the analysis. The size of the fruit crop recorded under the isolated *P. excelsa* parent trees ranged from 38 to 25,761 fruits. The seedling bank varied in size between 38 and 399 seedlings (overall from all trees = 1631 seedlings), with an overall average seedling density of 0.43 seedlings/m² (± 0.41 SD). The area of the seedling bank around the isolated *P. excelsa* trees averaged 730.4 m² (± 621.1 SD).

Spatial patterns of the seedling bank

Seedling distribution around the isolated parent trees is depicted in Fig. 2. The distribution of the seedling bank was apparently related to the slope, although we find no significant statistical correlation among descriptive traits of the seed and seedling bank and the slope. The tree #3 was exceptional in that most seedlings concentrated upslope to the parent tree. The remaining trees had the seedling bank distributed roughly following the terrain slope. Most trees, except tree #1, were located in an eccentric position regarding the seedling bank. In the trees #5 and 7 the distribution of the seedling bank seems to reflect the direction of the prevailing NE trade winds and at the same time the main slope (Fig. 2).

Trees # 1, 4 and 5 had all the recognized seedling size classes represented; trees # 2, 3, 7 and 8 had the three first size (age) classes (< 40 cm height), although there were a higher proportion of younger seedlings (class 1). The tree # 6 had only the first two age classes (classes 1 and 2) represented (Fig. 2).

The younger seedlings were differentially clumped around the parent tree base (mostly under the projection of the tree crown) in all the isolated trees, whereas the older seedlings clumped preferentially far from the parent tree (Fig. 2). For example, trees #2 and #3 had both seedlings in the class 1 clumped next to the parent tree and class 2 further from the parent tree.

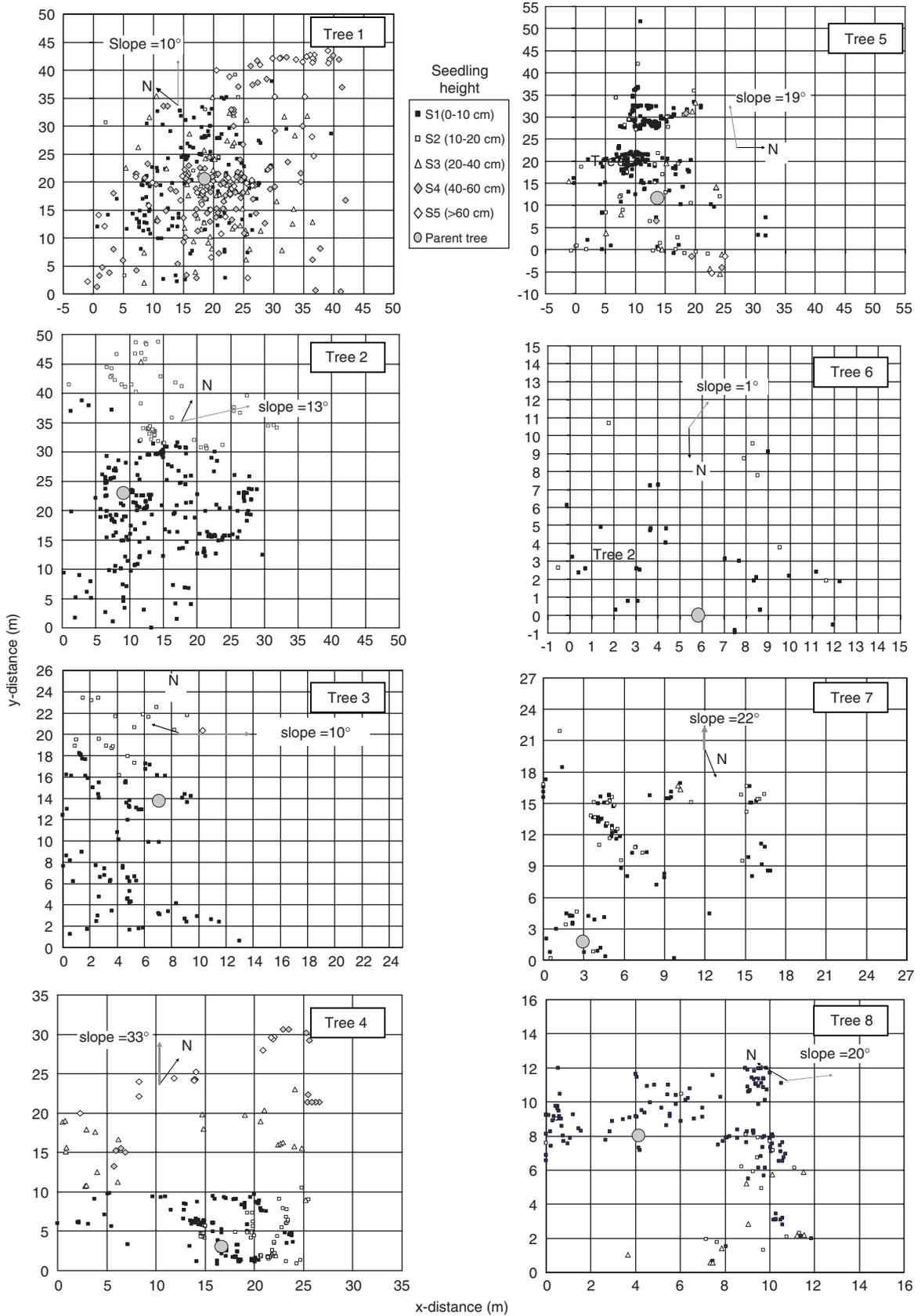


Fig. 2. Map of spatial location of the seedlings from each *Picconia excelsa* parent tree.

Correlation between seedlings size and distance to parent tree

Overall, a significant increase in seedling size (age) was found with increasing distance to parent tree (Table 1 and Fig. 3A). There were significant differences among

Table 1. Pearson correlations between seedling height and distance to parent tree in eight isolated *Picconia excelsa* trees

Tree number	Pearson's <i>r</i>	<i>p</i>	<i>n</i> ^a
1	0.264	<0.001	400
2	0.337	<0.001	289
3	-0.133	0.169 ns	108
4	0.880	<0.001	215
5	0.018	0.755 ns	315
6	0.535	0.001	38
7	0.209	0.033	104
8	0.380	<0.001	162
All trees	0.337	<0.001	1631

Significant correlations are shown in bold.

^a*n* = seedling number.

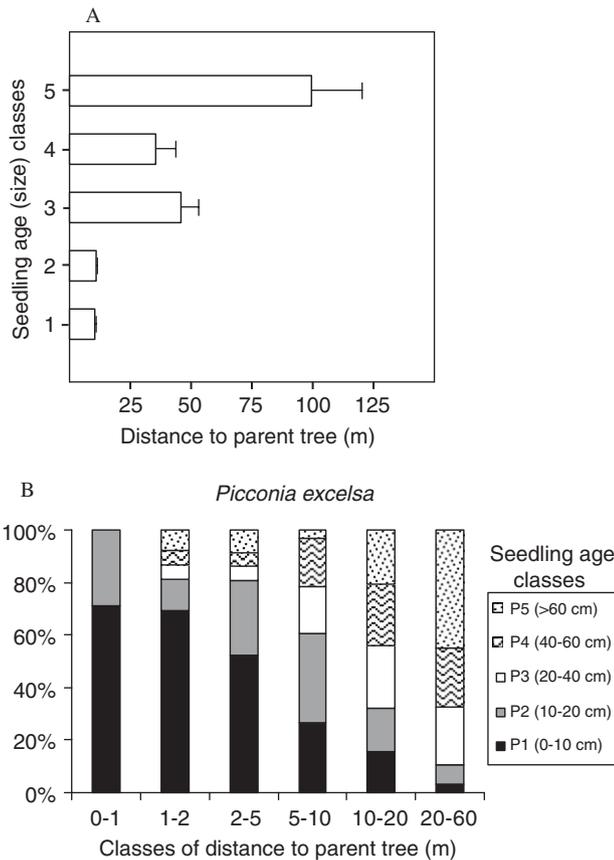


Fig. 3. Mean (+1SE) density of seedlings per age (height) class (A) and proportion of seedlings per age class (B) with distance to *Picconia* parent trees.

distances to parent tree in the number of seedlings per age class ($F_{4,1626} = 58.998, p < 0.001$) (Fig. 3b). Of the eight individual parent trees, six (except trees # 3 and 5) exhibited a significant correlation between seedling age and distance to parent tree (Table 1). A significant correlation was found between these two parameters for data from all trees combined (Table 1).

Apart from the mean seedling size (age), the area of the seedling bank was the other variable significantly selected by a regression model as correlated with the maximum distance to parent tree (Table 2 and Fig. 4). The larger the area occupied by the seedlings, furthest distances from the parent tree were reached by seedlings (Fig. 4). The variables parent tree height, diameter at breast height (DBH), total number of seedlings, seedling density and mean distance to parent tree were excluded from the model as not influential on maximum reach of seedlings.

The correlation between the canopy seed rain and the number of seedlings revealed no significant relationships among these parameters (for a $p < 0.05$).

Fruit (seed) vs. seedling pattern

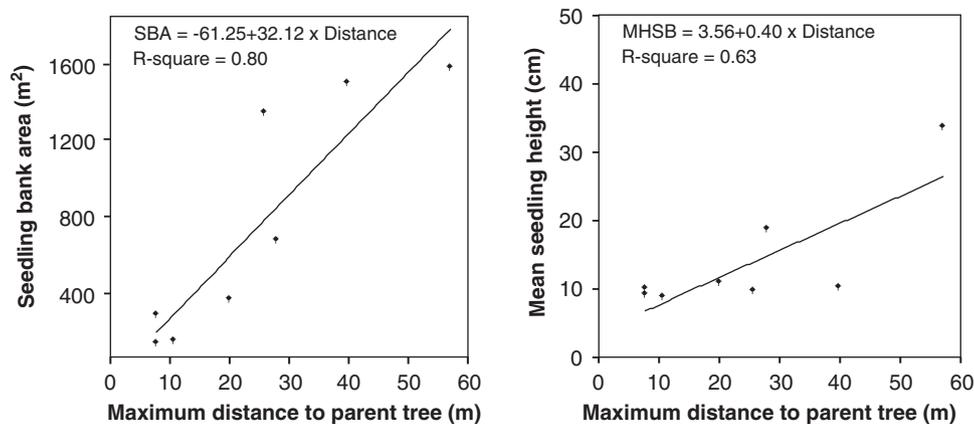
Across the eight parent trees, the seedlings reached much longer distances from parents than the fruits (seed shadow). Seed shadows disappeared completely within 15 m (mean \pm SD = 6.75 ± 4.33 m) from the parent trunk, but it can be noted that the bulk of seeds is deposited within the first 4 m below the parent tree crown (Fig. 5). Seedlings reached distances normally further than 30 m from the parent tree base, notably farther than the seed rain (Fig. 5). Seedling density decreased continuously to 9–25 m from the parent tree (mean \pm SD = 22.88 ± 10.88 m) at which point it decreased to almost zero seedlings per square meter. This indicates the average area where the bulk of seedlings from a parent tree could be found for this species (Fig. 5).

Discussion

To study correlations of spatial distribution of seedlings and thus regeneration patterns in laurel forest trees, it is necessary to investigate the offspring distribution regarding parent trees. This is only viable if the offspring can be ascribed to a given progenitor. Despite a labour-intensive search over the study area, we detected only a very small number of focal, adult isolated trees of *P. excelsa*. This tree species is relatively frequent, but it is abundant only locally, and in these cases, the trees are near from each other and relatively clumped. Aside scarcity of isolated trees, another caveat for our analyses was that two out of 10 isolated trees did

Table 2. Results of a regression model between the dependent variable (maximum distance of seedling to parent tree) and the independent variables (see Materials and methods)

Model	Sum of squares	df	Quadratic mean	<i>F</i>	<i>p</i>	<i>R</i> ²
<i>Variables included in step 1—seedling bank area</i>						
Regression	1661.33	1	1661.33	23.53	0.003	0.797
Residual	423.69	6	70.61			
Total	2085.02	7				
<i>Variables included in step 2—seedling bank area, mean seedling height</i>						
Regression	1973.95	2	986.98	44.43	0.0007	0.947
Residual	111.06	5	22.21			
Total	2085.02	7				

**Fig. 4.** Regression plots between the two explaining variables significantly selected by the regression analysis and maximum distance to parent tree (dependent variable).

not produce fruit crop in 2003 nor did present a seedling bank. This was surprising as *Picconia* is a hermaphroditic species, and these trees would potentially fruit and thus we should have been able to find seedlings recruited from past crops. All the remaining focal trees had a seedling bank.

The mere presence of seedlings in the understory is not an indicator of a persistent seedling bank, which can be detected only through monitoring (Marks and Gardescu, 1998). In a 5-year chronosequence in holm oak (*Quercus ilex*) in Spain, Gracia et al. (2001) concluded that the seedling bank was only a reserve of small individuals without a major effect in forest dynamics.

The values of seedling density were strikingly lower for *P. excelsa* (mean = 0.43 seedlings/m²) than for other studied laurel forest trees that have a seedling bank, such as *L. novocanariensis*, with up to 150–200 seedlings/m², *A. barbujana* and *P. indica* (Fernández-Palacios and Arévalo, 1998). The typical seedling density for *P. excelsa* was similar to that of *Viburnum rigidum* (Arévalo and Fernández-Palacios, 2003). Other authors

have reported much lower densities for *P. excelsa* (0.1 seedlings/100 m²) but not in relation to their parent trees (Shumiya et al., 1999).

Higher densities of seedlings might be related to potentially higher density-dependent predation rates, as would be the case (hypothetical) for the Lauraceae, and this process would be less intense in *Picconia* due to lower seedling density (Willson and Whelan, 1990). Many physical, chemical and biotic factors may act as filters on a plant's reproductive output between seed and seedling phases, and many plants suffer losses in their reproductive output before seedlings become established (Clark et al., 1999; Nathan and Casagrandi, 2004; Osunkoya, 1994).

The seedling recruitment pattern of *P. excelsa* is shown also by other laurel forest tree species, as *Heberdenia excelsa*, *R. glandulosa* and *Viburnum tinus* spp. *rugosum*. Instead of a seed bank, they have a bank of seedlings of different ages surrounding the parent tree after gravitational dispersal, which are able to grow under closed canopy, or they occur as isolated trees when dispersed by birds. Ship rats (*R. rattus*) predate

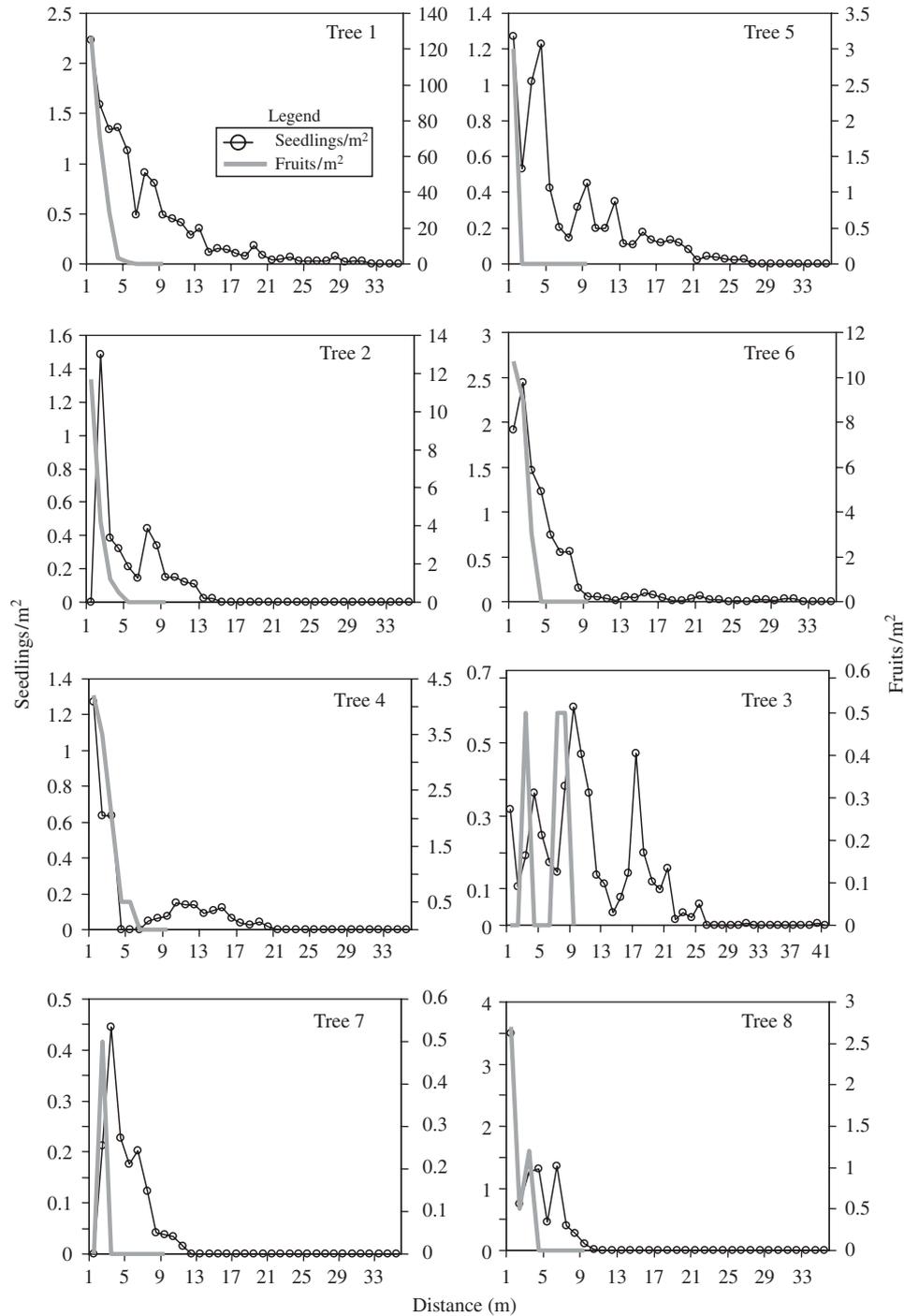


Fig. 5. Seed and seedling shadows from parent trees of *Picconia excelsa*.

huge amounts of fruits and leaves of *Picconia*, thus decimating its seed output (Bañares and Barquín, 1982; Juan D. Delgado, pers. obs.). Blackbirds (*T. merula*) have been observed to take fruits that they finally do not manage to swallow and are finally dropped to the ground, frequently just beneath the tree canopy (Juan D. Delgado, pers. obs.).

That older seedlings were found far from the parents, and the younger were located clumped under the tree crown, supports the idea that survival probability increases with distance to parent trees (distance hypothesis) (Janzen, 1970). This would cause a major dispersion and minimize clumping of the offspring, which could reduce attraction of herbivores, parasites and

disease vectors (Connell, 1979; Janzen, 1970). Similar phenomena have been observed previously in trees from tropical forests (Levins et al., 2003). In our study, the older *Picconia* seedlings (>60 cm height) seem to represent plants that have escaped predation (either by rats in the seed phase, or probably by the endemic slug *Plutonia lamarckii* and other invertebrates in the seedling phase). This could have occurred due to a longer distance from parent trees, which might favour escaping density-dependent predation or diseases (Augspurger, 1983b). Nevertheless, we could not discriminate between declining establishment and decreased survival with distance. Both may be causes for the observed decrease in seedling number from seed source (Nathan and Casagrandi, 2004). Further analysis including distances of dispersal, germination and establishment sites and predator movements (of long-distance predators, such as rats, and short-distance predators, such as invertebrates), and predation distances regarding parent trees, could shed further light on the observed seedling patterns (Nathan and Casagrandi, 2004).

The studied trees and their seedling cohorts presented well structured age pyramids in which the younger classes dominate over the high growing ones. This is interpreted as quite a high mortality in the first stages of growing of the seedlings. This implies that the seedlings surviving and advancing to older classes would be the exception rather than the rule. The tree #1 is uncommon since its age pyramid is inverted, and this is interpreted as a high mortality of intermediate age classes due to some environmental event, may be a previous intense drought.

In all the focal trees, we consistently detected a different distribution of seeds (fruits) and seedlings, with seedlings reaching much longer distances from the parent tree than fruits, which were limited to the limits of the crown projection. The fruits of *Picconia* can move away from the parent tree to the germination sites following the slope by gravity, by rain or by frugivores. Also, the older seedlings located in farther positions can come from various seed rain events, but the fruits we counted are only those from the year of study, so we cannot correlate seed rain and seedling distribution. Gravity itself may play a greater role concentrating seeds directly around parent trees, and bird dispersers and slope (through the action of gravity) would be responsible for seeds reaching distant sites, as suggested by the furthest seedlings. It is known that bird dispersers play an important role in the distribution of the fruits and seeds of *Picconia* (Delgado and Valido, 1998; Martín et al., 2000; Valido and Delgado, 1996), as well as in other Oleaceae (i.e. *Olea*, Rey and Alcántara, 2000). In addition to the high potential of bird dispersers, we found a noticeable trend of spatial distribution of the seedling bank following also the prevailing physical forces (NE trade winds and slope of the terrain).

The younger seedlings were clumped tightly around the parent trees because the fruit rain is maximal there, and thus the highest number of germinations occurs (Fig. 3A and B). We hypothesize several possible causes for the observed absence of older (taller) seedlings just beneath the parents, and conversely, for presence of a sparse population of older recruits far from the parent trees. First, once the seedlings exhaust the reserves stored in the seed, they begin to absorb nutrients and water through the developing root system. At this point, competence with other conspecific seedlings of the same cohort and with the parent itself starts. Second, allelopathic compounds present in leaves from the parent plant can influence the seedling growth negatively (González-Coloma et al., 1990; Rice, 1984). Since the position of older seedlings relative to the parent position was preferentially far away, and since conspecific density decreases, the competence of this population to recruit with conspecifics of similar age diminishes, and with the parent tree probably disappears.

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