Effects of thinning on throughfall in Canary Islands pine forest — the role of fog

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Abstract

Throughfall was monitored over a one-year period in a 48-year-old *Pinus canariensis* plantation on the northern side of the island of Tenerife, nine years after light thinning (mean 15% of basal area (BA)) or heavy thinning (mean 56% of BA). Three plots of each treatment (light thinning, heavy thinning, no thinning) were studied, using a randomized block design. Mean total throughfall over the year of study was about 2.0 times the incident rainfall in the control plots, about 2.2 times rainfall in the lightly thinned plots, and about 1.8 times incident rainfall in the heavily thinned plots. The high throughfall-to-rainfall ratios are as expected, given the importance of fog entrapment in these forests. The statistical analysis indicated that the observed differences in throughfall are attributable to the treatments, not to plot topography. Throughfall showed significant relationships with actual BA, surface roughness (as tree height variability) and leaf area index (LAI), all of which varied significantly among treatments (as expected). Our results are unexpected as heavy thinning led to a long-term decline, not increase, in throughfall. The explanation for this result is the importance of fog entrapment may mean that reducing LAI and surface roughness (height variability) has a negative effect on throughfall. The long period elapsed between thinning and throughfall estimation means that LAI of light thinning plots exceeded pre-thinning values, and then throughfall values. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Vegetation cover has a profound influence on the hydrological cycle. A proportion of precipitation is intercepted by the vegetation, and some of this is lost to the atmosphere by evaporation. As a result of differences in interception losses (i.e. evaporation of intercepted rainfall), forest canopy characteristics are a principal cause of hydrological differences between watersheds, and notably differences in runoff times and runoff volumes (Gash et al., 1980; Lloyd et al., 1988). An understanding of relationships between canopy characteristics and interception is thus essential for quantitative prediction of the effects of deforestation (Gash et al., 1980) and changes in land use and vegetation (Bosch and Hewlett, 1981).

Thinning (i.e. the removal of a certain number of trees) leads by definition to a reduction in canopy

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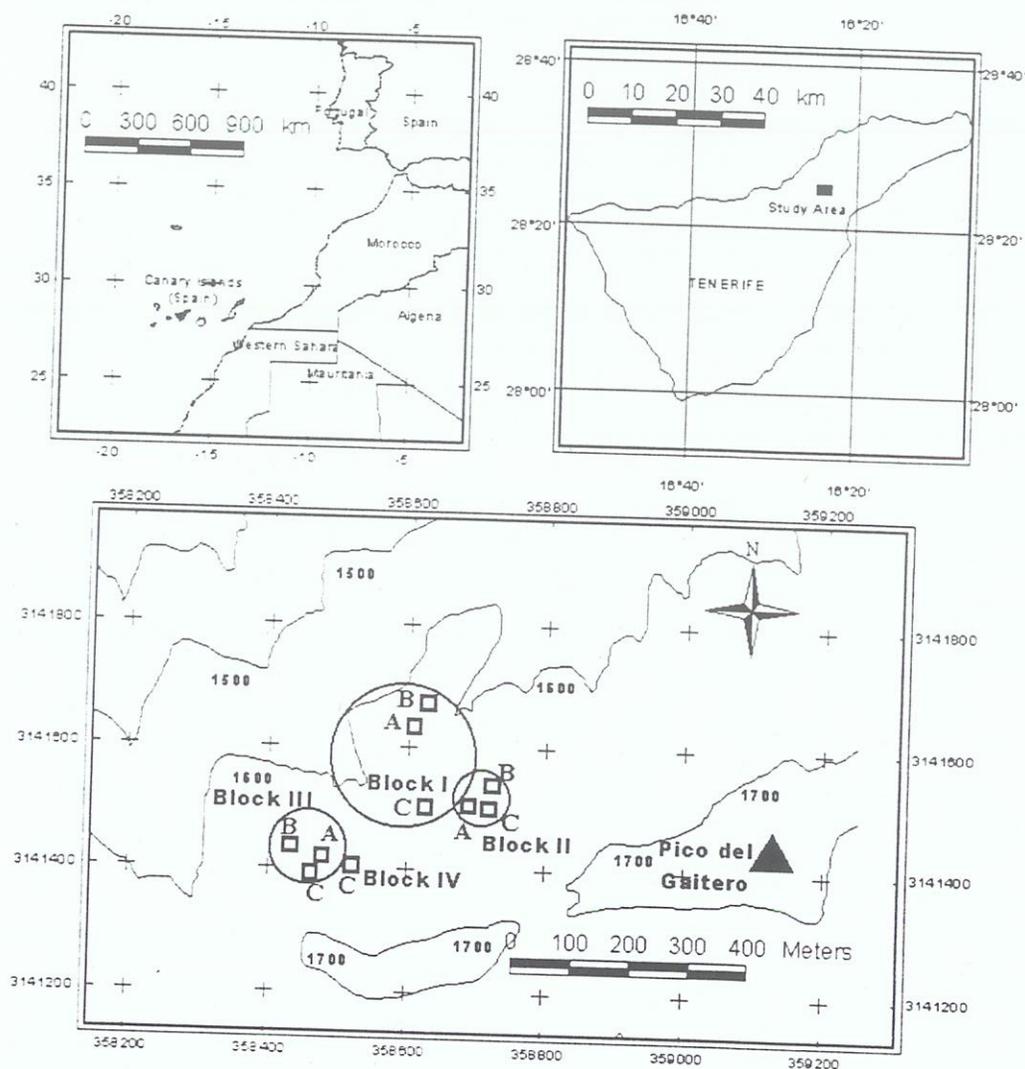et al.,
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Fig. 1. Maps showing the location of the Canary Islands in Macaronesia, the location of Tenerife in the Canary Islands, and the location of the study area in Tenerife. Map of the study area, showing the locations of the 10 study plots.

density, and may thus have marked effects on runoff times and volumes, particularly in environments in which interception losses are important (Teklehaimanot et al., 1991).

Various authors have quantified the effects on water balance of thinning of conifer stands (Veracion and López, 1976; Aussenac and Boulangeat, 1980; Aussenac et al., 1982; Aussenac and Granier, 1988; Crockford and Richardson, 1990; Teklehaimanot and Jarvis, 1991; Teklehaimanot et al., 1991), deciduous

stands (Aussenac and Boulangeat, 1980; Bréda et al., 1995) and mixed stands (Baümler and Zech, 1997). In most of these studies thinning involved removal of 50% of basal area. In all cases, throughfall increased after thinning, while stemflow and evaporation losses due to interception decreased (though not in proportion to the amount of biomass removed). However, most of these studies continued for less than two years, with the maximum study duration being five years (Aussenac and Granier, 1988). The

medium- and long-term effects of thinning are poorly understood.

Following the Spanish conquest of the island of Tenerife at the end of the 18th century, the island's pine forests were massively felled for the sugar industry and shipbuilding, with the affected land subsequently being used for agriculture and livestock. By contrast, the period 1940–1987 saw large-scale reforestation. Currently, forest management techniques are being applied to the reforested stands, without a clear understanding of the effect of the different measures on water balance, which is in itself poorly understood on this island (Kämmer, 1974). In the present study, we quantified the effects of thinning cuts of different intensity on throughfall and water balance in a *Pinus canariensis* plantation, nine years after thinning. We attempted to relate the observed changes to changes in canopy characteristics, and investigated the possible effects of plot topography.

2. Material and methods

2.1. Study area

The study area is located 1 km southwest of Pico del Gaitero, a mountain in the north of Tenerife (1747 m a.s.l.), in the La Corona Forestal National Park (Fig. 1). The study area (Fig. 1) was replanted in 1950.

Mean temperature over the period 1986–1994, as measured at the nearby weather station at the top of the mountain (Pico del Gaitero) maintained by the Instituto Nacional de Meterología, was 12.6°C, with an absolute maximum of 31.2°C and an absolute minimum of −4.2°C. Mean relative humidity over the same period was 52%, with high within-year variation. Monthly mean maximum relative humidity was above 70% in all months except July and August. Previous rainfall data are not available for this weather station.

2.2. Experimental plots

The experiments were done in a plot covering a total area of 900 m² (30 × 30 m), in which controlled thinning was performed in 1988 for research purposes. Within this area, we marked out and used a plot covering a total area of 400 m² (20 × 20 m), with the aim of minimizing edge effects.

2.2.1. Thinning

The thinning, performed in 1988, was of two types, hereinafter referred to as treatments A and B. Treatment A ("light thinning") involved removal of 35 ± 4% of dominated trees, corresponding to 15 ± 3% of basal area. Treatment B ("heavy thinning") involved removal of 66 ± 6% of dominated or intermediate trees, corresponding to 58 ± 3% of basal area, in no case modifying the dominant layer. Control plots (treatment C) were not subjected to thinning, except for removal of dead trees.

A total of 10 plots were included in the study (three for each treatment, four control plots). These plots were grouped into three blocks in different topographic positions. Each block (blocks I–III) contained one plot of each type; block IV, on the ridge dividing two gullies, consisted of a single control plot.

2.2.2. Topographic characterization of the experimental plots

For each plot we determined maximum slope and orientation of maximum slope (Table 1). The precise locations of the four corners of each plot were determined with a GPS device. From the resulting digital map (ArcView 3.1 Spatial Analyst ESRI; pixel size 5 m²), we then determined mean slope, mean altitude and orientation (Table 1). On the basis of orientation, we calculated degrees difference with respect to a wind-rose with 30° divisions.

2.2.3. Cover estimation

Cover-related variables were measured before thinning, immediately after thinning, and 9 years after thinning (Table 2). The variables determined were stand density (trees per ha), mean diameter at breast height (DBH), quadratic mean diameter, mean DBH of dominant trees, basal area (BA), mean height (h), and top height (height of dominant trees, h_0). The tree height variability was estimated as $h_0 - h$.

Leaf area index (LAI) was estimated 9 years after thinning with a Li-Cor LAI-2000 device (Li-Cor Inc.). Measurements were made on 6 June 1997, at dusk, with a 180° shutter: one measurement was taken in the center of a nearby clearing, and ten measurements were taken in the center of the plot, in all cases ensuring that the unshuttered half of the lens pointed towards the center of the plot, and eliminating measurements obtained at 4 and 5°. The measurements were then

Table 1
Topographic characteristics of the ten plots

	Block/thinning type	Control (C)	Light thinning (A)	Heavy thinning (B)
Maximum slope (°)	I	12	13	14
	II	16	19	19
	III	22	24	21
	IV	20	–	–
Mean slope (°)	I	10.7 ± 1.7	10.6 ± 1.7	9.7 ± 1.5
	II	14.9 ± 2.4	14.9 ± 2.4	16.8 ± 2.7
	III	20.3 ± 3.3	21 ± 3.4	19.9 ± 3.2
	IV	19.3 ± 3.1	–	–
Orientation of maximum slope (°)	I	175	311	314
	II	168	145	185
	III	210	210	202
	IV	175	–	–
Mean orientation (degrees difference with respect to 360°)	I	26 ± 4	98 ± 16	95 ± 15
	II	17 ± 3	53 ± 9	21 ± 3
	III	40 ± 6	47 ± 8	24 ± 4
	IV	22 ± 4	–	–
Altitude (m a.s.l.)	I	1643	1620	1620
	II	1648	1643	1638
	III	1665	1653	1658
	IV	1653	–	–

interpolated with a second measurement in the clearing. The values obtained were corrected for plot slope. In addition to LAI, this instrument also allows estimation of DIFN (fraction of the sky visible beneath the canopy) and MTA (mean tilt angle of foliage).

2.3. Measurement of throughfall

Throughfall was measured at 1- to 3-week intervals (generally weekly) starting on 15 March 1997 and finishing on 3 April 1998, using a total of 70 collectors (7 per plot; total area 15888 cm^2) that were maintained in the same positions throughout the study. Each collector comprised a 17-cm-diameter funnel with high parallel walls, feeding into a 5-liter bottle. The collection surface was located 70 cm above the ground. The seven collectors in each plot were positioned at random within a 1 × 1 m grid superimposed on the plot. At each visit, the volume of water in each bottle was determined with a set of measuring cylinders (25, 50, 100 and 1000 ml).

2.4. Statistic analyses

All analyses were performed with the aid of SPSS version 7.5. To investigate variation among plots in weekly throughfall and in total throughfall, we first performed two-way analyses of variance (factors *treatment* and *block*). If no significant effect was detected, we performed one-way analyses of variances with factor *treatment* or *block*, then pairwise comparisons by Tukey least significant difference tests. Before analyses of variance, data normality was in all cases confirmed using Lilliefor's modification of the Kolmogorov–Smirnov test. If this test indicated that normality could not be assumed, the data were subjected to logarithmic or square-root transformations, as recommended for situations of this type by Lloyd and Marques (1988).

In regression analyses, we tested all models available in SPSS version 7.5, in all cases selecting which gave the highest observed/expected correlation, though excluding models in which the Durbin–Watson test indicated correlation of residuals. Unless

Table 2
Canopy structure characteristics of the ten plots, after thinning and 9 years after thinning

	Block	Control (C)		Light thinning (A)		Heavy thinning (B)	
		After thinning	After 9 years	After thinning	After 9 years	After thinning	After 9 years
Number of trees per ha	I	1072	1056	656	656	288	288
	II	1232	1168	912	912	368	368
	III	1082	1056	656	656	496	496
	IV	992	992	–	–	–	–
Mean DBH (cm) all trees	I	27.2	29.3	30.9	34.2	32.2	36.9
	II	26.3	28.1	28.9	30.3	30.8	34.7
	III	25.4	27.1	30.3	32.3	25.4	28.1
	IV	27.0	28.6	–	–	–	–
Mean DBH (cm) dominant trees	I	36.7	40.2	37.5	41.4	37.8	41.4
	II	35.7	38.8	37.7	40.2	36.3	40.8
	III	35.3	38.2	39.3	42.2	31.6	34.1
	IV	36.9	39.2	–	–	–	–
Top height (m)	I	18.3	20.9	20.0	22.6	19.1	22.3
	II	20.3	21.4	21.2	22.9	19.4	20.9
	III	20.7	22.3	20.1	21.8	19.1	17.7
	IV	19.5	20.3	–	–	–	–
Mean height (m) all trees	I	16.3	18.5	20.0	20.8	18.9	21.3
	II	17.8	18.9	18.6	19.5	18.3	20.3
	III	17.9	19.5	19.4	19.6	16.8	17.4
	IV	17.6	18.8	–	–	–	–
Basal area (m^2 ha^{-1})	I	62.4	71.4	49.2	61.5	23.4	30.8
	II	67.0	73.2	59.7	68.0	27.4	34.9
	III	55.1	60.9	47.3	56.2	25.1	30.8
	IV	56.6	63.6	–	–	–	–
LAI (m^2 m^{-2})	I	–	3.25 ± 0.09	–	3.90 ± 0.06	–	2.84 ± 0.09
	II	–	3.53 ± 0.14	–	3.34 ± 0.14	–	2.24 ± 0.08
	III	–	3.18 ± 0.12	–	3.67 ± 0.17	–	2.05 ± 0.13
	IV	–	3.09 ± 0.09	–	–	–	–
Mean tilt angle of foliage (°)	I	–	53 ± 0	–	57 ± 2	–	55 ± 2
	II	–	59 ± 0	–	55 ± 4	–	55 ± 7
	III	–	60 ± 1	–	47 ± 0	–	51 ± 4
	IV	–	60 ± 2	–	–	–	–

otherwise stated, statistical significance is taken to be indicated by $p < 0.05$.

3. Results

3.1. Variation over time in rainfall and throughfall

Rainfall during the study period was lower than normal, with a total of 439.9 mm measured at the Pico del Gaitero weather station over the period 12 March 1997–6 April 1998. This total was not uniformly distributed: a rainy May/April 1997 (185.2 mm) was followed by a dry May/June (35.5 mm), then a long drought over the period July–September, then fairly uniformly high rainfall over the period October–January (84.4 mm), then a dry February/March, and finally 32.5 mm at the beginning of April 1998.

Fig. 3 shows mean throughfalls during each 1- to 3-week interval of the study period for which non-zero throughfalls were obtained, in plots grouped by
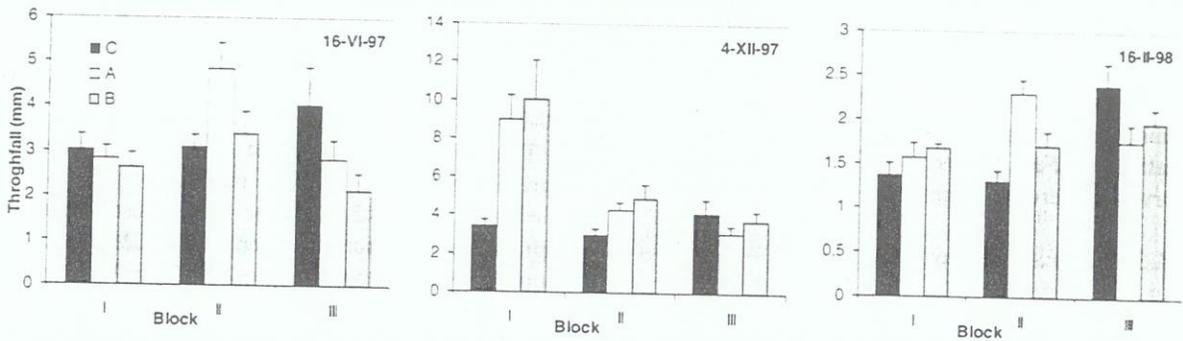
Fig. 2. Mean throughfall in the 9 plots (excluding the block-IV control plot), for the three measurement intervals in which analysis of variance (factors *block* and *treatment*) indicated a significant interaction between the two factors.

treatment. Throughfall was not detected mostly during the summer months.

3.2. Variation in plot topography and canopy structure

Plot topography and treatment appeared to be uncorrelated. However, significant among-block differences were detected in maximum slope ($F = 12.25$, $p = 0.008$, d.f. $= 2.8$), altitude ($F = 9.098$, $p = 0.015$, d.f. $= 2.8$) and mean slope ($F = 125.56$, $p < 0.0005$, d.f. $= 2.8$). Tukey tests indicated signif-

icant differences in maximum slope and altitude between blocks I and III, and significant differences in mean slope between all three blocks.

Conversely, analyses of variance revealed a significant variation in canopy structure variables among treatments but not among blocks. Specifically, significant among-treatment differences were detected in basal area ($F = 39.724$, $p < 0.0005$, d.f. $= 2.8$), DIFN ($F = 8.803$, $p = 0.016$, d.f. $= 2.8$), LAI ($F = 13.554$, $p = 0.006$, d.f. $= 2.8$) and tree height variability ($F = 5.813$, $p = 0.047$, d.f. $= 2.8$). In all cases, Tukey tests indicated significant
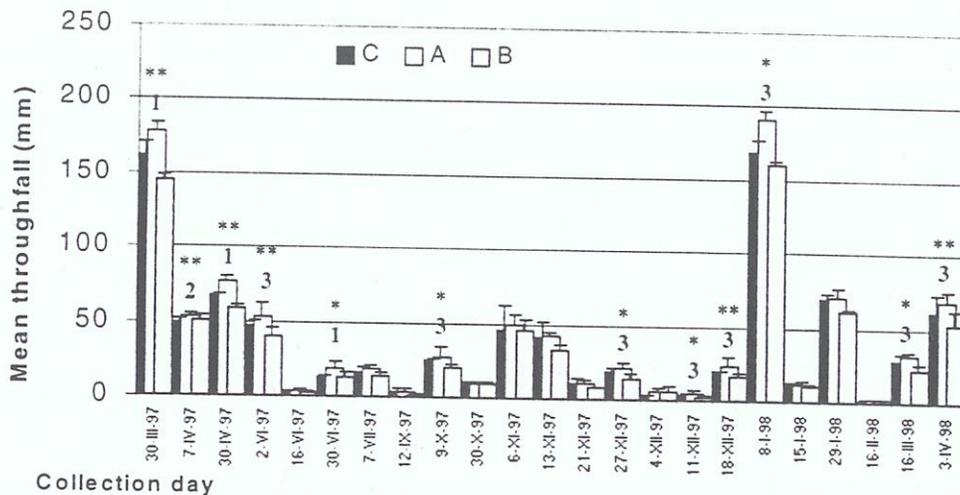

Fig. 3. Mean throughfall in plots of each treatment (A, B, and C) as recorded in each measurement interval over the study period. Asterisks indicate significant among-treatment variation (*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$). Numbers summarize the results of Tukey tests: 1 = significant differences between A and C, and between A and B; 2 = significant difference between A and C only; 3 = significant difference between A and B only. Note that the throughfall ranking was A > C > B for all intervals except those ending 7XI-97 (A > B > C), 30-VI-97 (A > B > C) and 4-XII-97 (B > A > C).

differences between treatments A and B, and between B and C.

As expected, given the nature of the experiments, number of trees per ha varied significantly between treatments ($F = 30.569$, $p = 0.001$, d.f. = 2, 8; all pairwise differences significant).

3.3. Variations in throughfall

The statistical analysis shows that the variability in throughfall in the periods 16-VI-97 ($F = 2.958$, $p = 0.028$, d.f. = 4, 62), 4-XII-97 ($F = 4.616$, $p = 0.003$, d.f. = 4, 62) and 16-II-98 ($F = 6.790$, $p < 0.0005$, d.f. = 2, 60) (Fig. 2) is primarily related to significant *block × treatment* interactions. With the data available for our relatively short study period, there is no clear explanation for these interactions. However, it is worth pointing out: (a) that in all three intervals throughfall in the control treatment C was higher in block III than in the other two blocks; and (b) that in all three intervals total throughfall was very low. Mean throughfall in treatment-B plots was higher than in treatment-A plots only in the interval ending 4-XII-97. These data are not used in further analysis.

3.3.1. Among-block variation in throughfall

The ranking of total throughfall over the study period was II > III > I. Means ± SD ($n = 3$ plots per block) were 919.3 ± 66.7 mm for block II, 878.0 ± 48.5 mm for block III, and 852.3 ± 58.7 mm for block I. The maximum difference between block means was thus 67 mm. So systematic differences between blocks are statistically insignificant.

3.3.2. Among-treatment variation in throughfall

Among-treatment variation in throughfall, unlike among-block variation, showed a clearly defined pattern: in all intervals considered throughfall was highest in treatment-A plots. In 18 of the 20 intervals, the throughfall ranking was A > C > B; the Tukey tests indicated significant differences between A and B in 10 of these intervals, and between A and C in two intervals (see Fig. 3). In 2 of the 20 intervals, the throughfall ranking was A > B > C; the Tukey tests indicated significant differences between A and C in both intervals, and a significant difference between A and B in one of the intervals. A significant difference between B and C was not detected in any of the

20 intervals. Significant between-treatment differences were detected in all intervals in which throughfall was high (>50 mm), except the interval ending 29-I-98.

Total throughfall over the study period likewise varied significantly among treatments ($F = 4.526$, $p = 0.015$, d.f. = 2, 60). The Tukey tests indicated significant differences between A and B. Means ± SD ($n = 3$ plots per treatment) were 977.8 ± 38.1 mm for treatment A, 791.3 ± 22.3 mm for treatment B, and 880.3 ± 27.1 mm for treatment C. The percentage difference with respect to the control treatment C was thus −11.1% for treatment A and −10.1% for treatment B. Throughfall-to-rainfall ratios were 2.22 (A), 1.80 (B) and 2.00 (C).

3.4. Relationships between throughfall and plot characteristics

Linear regressions of total throughfall on plot topography variables in no case indicated a significant relationship. This indicates that topography has no major effects on throughfall in the plots studied, with the exception discussed below.

However, linear regressions of total throughfall on canopy structure variables (Fig. 4) indicated that basal area, LAI and tree height variability all had significant effects at the 5% level. It should be noted that all three variables differed significantly between treatments, and thus these variables might be responsible for the observed among-treatment differences in throughfall.

The single block-IV plot (treatment C) showed much higher throughfall (2.78 times rainfall) than the other three control plots. This may be attributable to microtopographic conditions that are difficult to quantify, since this plot is situated on a narrow ridge between two steep-sided gullies, probably leading to aspiration of wet air masses and consequent modification of microclimatic conditions. In view of the atypical behavior of this plot, it was excluded from the analyses.

4. Discussion

The observed among-plot variations in throughfall appear not to be due to differences in topography, despite the existence of significant differences of this type, since (a) throughfall did not vary significantly
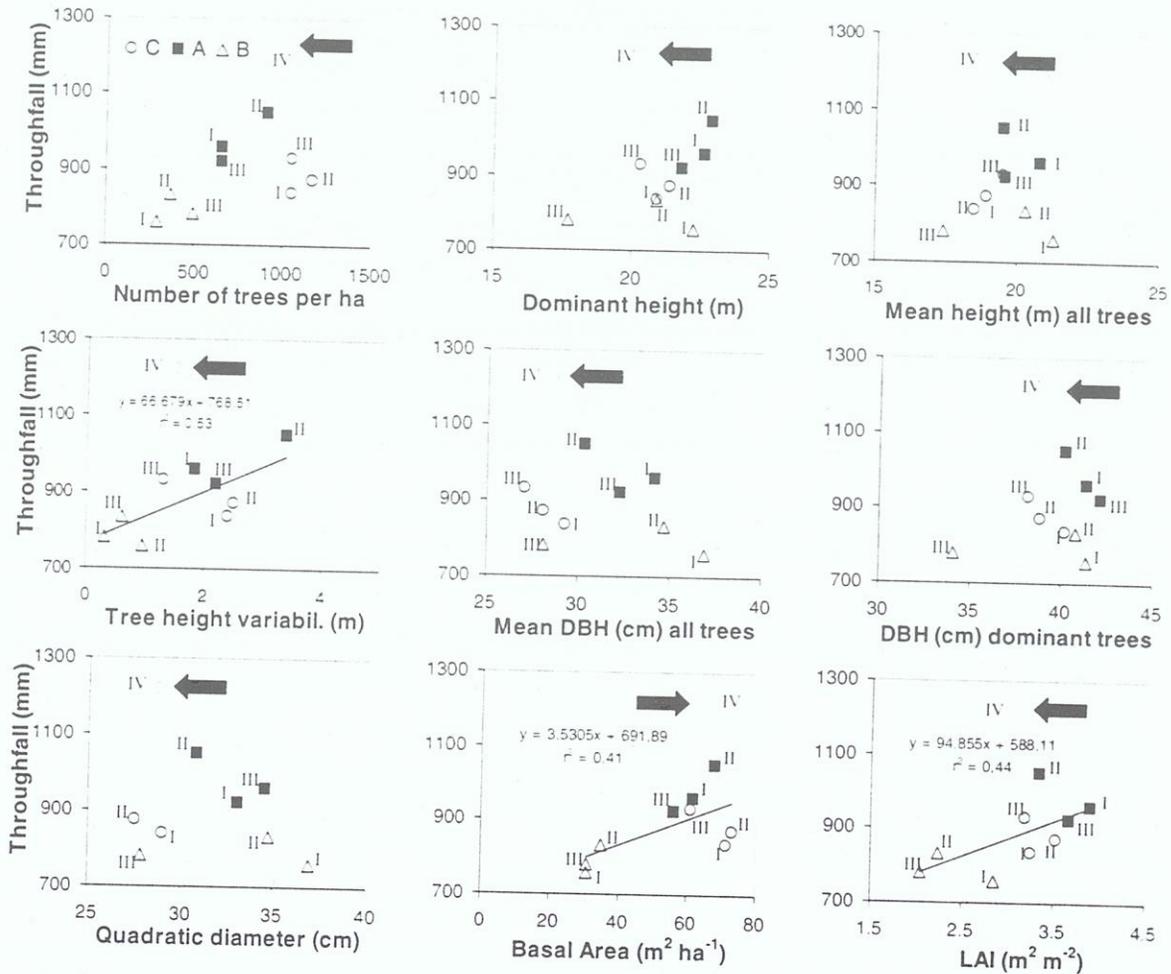
Fig. 4. Plots of total throughfall over the year of study against canopy structure characteristics, showing regression lines where significant. Each point represents a single plot; the Block-IV control plot is indicated with an arrow.

among blocks, either considering individual intervals (except in three of the 20 intervals considered) or the total for the whole study period and (b) there was no significant relationship of total throughfall on plot topography variables. However, two-way analysis of variance indicated significant interactions between topography and plot structure. Furthermore, topographic variables almost certainly have a significant effect on throughfall in topographically atypical plots such as the block-IV control plot. By contrast, canopy structure variables had a clear effect on throughfall, with marked and significant among-treatment variation in throughfall, and significant correlations between throughfall and the canopy structure vari-

ables basal area, LAI and tree height variability. In what follows, we thus focus on the effects of crop structure variables on throughfall.

Our results are unexpected in that, while light thinning (treatment A) led to an increase in throughfall, heavy thinning (treatment B) led to a decline. Previous studies have in all cases reported an immediate increase in throughfall, and a decline in interception and stemflow, following thinning (Table 3). However, these previous studies have indicated that the degree of decline in interception is not proportional to the amount of biomass removed or to the increase in between-tree spacing. If interception and canopy storage were closely related, we would expect

Table 3
Summarized results of previous studies of the effects of thinning on interception: SV = stem volume, BA = basal area, 'Control' values are for the non-thinned control plots at the same time; 'Pre-thinning' values are for the thinned plots before thinning

	Forest	Rainfall (mm)	Age (years)	Treatment	Trunks ha^{-1}	BA (m^2 ha^{-1})	Interception as % rainfall
Veracion and López, 1976	Pinus kesiya	3601	30	Unthinned	–	32	13.5
				Thinned (50% BA)	–	16	11.0
Aussenac et al., 1982	Pseudotsuga menziessii	384.4	19	Control	2392	39.3	43.3[a]
				Thinned (50% BA)	1447	19.9	30.3[a]
Aussenac and Granier, 1987	Pseudotsuga menziessii	382.3[b]/53[c]	19	Control	2392	39.3	31.0[b]/60.8[c]
				Thinned (50% BA)	1447	19.9	23.0[b]/51.6[c]
Crockford and Richardson, 1990[d]	Pinus radiata	164[d] 166[d]	20	Unthinned	1708	35.1	20.9
				Thinned (50% BA)	700	17.4	12.2
Teklehaimanot et al., 1991	Picea sitchensis	441.78[e]	19	Control (spaced 2m)	3000		28.14
				Tree spacing 4 m	625		22.06
				Tree spacing 6 m	277		13.35
				Tree spacing 8 m	156		8.83
Breda et al., 1995	Quercus petraea		43	Control	3352	24.6	23[a]–17[b]
				Thinned (35% BA)	3077	17.6	16[a]–17[b]
Baumler and Zech, 1997[c]	Picea abies, Abies alba, Fagus sylvatica	1700–2500		Control		56.2	29.8
				Unthinned		50.9	26.6 (24–32)
				Thinned (-40% SV)			18.1

[a] Over the year after thinning.
[b] Over the two years following thinning.
[c] Over the four years following thinning.
[d] Over the study period.
[e] Over the 17 weeks following thinning.

that removal of $x\%$ of biomass (for example) would lead to a $\sim x\%$ reduction in interception; however, the observed decline in interception is in fact less than $x\%$. For example, one year after removal of 50% of basal area, the observed decline in interception (with respect to pre-thinning or control-plot values) was 18.5% (Veración and López, 1976), 30.2% (Aussenac et al., 1982) or 41.6% (Crockford and Richardson, 1990). Likewise, one year after removal of 35% of basal area, the observed decline in interception was 30.4% (Bréda et al., 1995). However, a directly proportional effect was reported by Baümler and Zech (1997), who obtained a 39.3% decline in interception one year after removal of 40% of trunk volume. Crockford and Richardson (1990) reported that the degree of disproportion depended on rainfall amount: for small rainfall events, the decline in interception observed one year after removal of 50% of basal area was close to 50%, whereas for larger events (>15 mm) the decline in interception was only about 30%. In the present study we did not determine interception directly, and in fact interception calculated as *Rainfall–Throughfall*, assuming stemflow to be negligible (as justified for this woodland type by Kämmer, 1974), was negative. However, removal of 15% of basal area led to a reduction of 11.1% in interception as calculated in this way, while removal of 56% of basal area led to an increase of 10.1%.

There are a large number of possible explanations for our unexpected results, in all cases relating to possible causes of the lack of proportion between biomass removed and interception. First, thinning will lead to greater wetting of the canopy, since a greater proportion of canopy storage capacity will be filled (Crockford and Richardson, 1990). Second, thinning will increase ventilation, leading to an increase in evaporation during rainfall (Rutter et al., 1971; Crockford and Richardson, 1990; Teklehaimanot et al., 1991), and possibly inducing increased interception by the individual trees remaining (though not by the plot as a whole). Third, thinning will modify the proportion of free rainfall in throughfall (Teklehaimanot et al., 1991). Fourth, thinning leads to an increase in incident solar radiation, and thus in evaporation (Crockford and Richardson, 1990). Fifth, thinning may lead to increased interception of fog (Teklehaimanot et al., 1991). Sixth, nine years elapsed between thinning and the throughfall determinations of the present study. Seventh, thinning may not have been entirely homogeneous.

All of these effects can be expected to be more pronounced after large rainfall events, after which the free surface of water available for evaporation is much higher (Crockford and Richardson, 1990). After smaller events, the degree of canopy wetting is lower, and the water present is more dispersed and less available for evaporation.

Of the seven possible explanations mentioned, only three might explain the observed difference between the present and previous studies, namely explanation 5 (increased fog entrapment), explanation 6 (the time elapsed between thinning and throughfall determination) and explanation 7 (non-uniform thinning). The latter two explanations relate to changes in canopy characteristics, notably LAI and leaf biomass, that alter the relationship of LAI to basal area removed. Such modifications may be attributable to the time elapsed between thinning and throughfall determination (explanation 6), or to the nature of the thinning itself (explanation 7). Possibly for these reasons, many thinning experiments have shown that interception is not proportional to stand density (Rutter, 1968; Aussenac and Granier, 1988; Stogsdill et al., 1989; Bréda et al., 1995).

The forest hydrology of the western Canary Islands is highly atypical, as illustrated for example by our observations that throughfall is more than two times rainfall. Similar results were obtained by Kämmer (1974) for the same area of forest: for example, at the nearby sites of La Cumbre (1590 m a.s.l.) and La Laguneta Alta (1447 m a.s.l.), this author obtained throughfall-to-rainfall ratios of 4.84 ($T = 3222$ mm, $P = 666$ mm) and 1.48 ($T = 425$ mm, $P = 288$ mm), respectively. These greater-than-one throughfall-to-rainfall ratios are attributable to interception of small fog droplets (0.001–0.5 mm) with velocities of less than 0.3 m s^{-1}, which float in the air and are thus transported by wind. The seasonality of the observed between-treatment differences may possibly reflect seasonal differences in the importance of fog interception, in turn reflecting seasonal variations in the mean height of the cloud ceiling (which rises with polar maritime air and sinks with Saharan continental air): over the period June–September, the mean height of the cloud ceiling is about 1350 m (considerably lower than the altitude of the plots considered in

the present study), while during the winter it rises to over 1600 m (Huetz de Lemps, 1969; Kämmer, 1974). This means that the mean number of hours with 100% relative humidity is highest in October/November, followed by December, March and May, and lowest over the period June–September, as revealed by the records of the Pico de El Gaitero weather station (Marzol et al., 1988). Furthermore, the periods of high relative humidity tend to be the periods of highest throughfall: this may be partially due to fog precipitation, which as a result of among-canopy differences may be responsible for the differences in throughfall.

The atypical results obtained for the single block-IV plot may likewise be attributable to this fact, since the aspiration effects acting on this plot may mean that the amount of fog passing through this plot is higher than through the other plots, leading to greater throughfall.

This may also explain the observed relationships between throughfall and LAI, and between throughfall and tree height variability. In systems in which water balance is largely dependent on interception, canopy storage capacity can be expected to increase with LAI (Ashton, 1979; Herwitz, 1985), so that increasing LAI will lead to increased interception and reduced throughfall. In our system, however, water balance is heavily dependent on fog interception, so that throughfall will increase with increasing LAI and increasing tree height variability (since increases in these variables mean increased surface area for fog entrapment). It is likely that interception losses may also increase with increasing LAI. Since LAI and tree height variability are higher in treatment-A plots, throughfall is expected to be highest in these plots. Deliberate maximization of throughfall is probably best achieved by modification of LAI and tree height variability. By consequence the increase of fog interception with LAI is expected to exceed the increase of interception with LAI.

As regards the time elapsed since the treatment, Crockford and Richardson (1990) have suggested that the duration of changes in interception rate will depend on the persistence of the change in canopy structure. According to these authors, the effect on interception will become increasingly small, until the trees reach the same cover and biomass as those existing prior to thinning. Clearly, thinning is accom-

panied by an immediate drop in LAI, typically followed immediately by a sharp increase, in both conifers (Bréda et al., 1995) and broad-leafed deciduous species (Vertessy et al., 1996): though note that in some species (oak, for example; Bréda et al., 1995) this behavior is not observed. The post-thinning increase in leaf biomass has been cited by Aussenac et al. (1982) as the explanation for the lack of relationship between percentage of basal area removed and decline in evapotranspiration. In general, the effects of thinning on interception indeed decline over time. For example, Aussenac and Granier (1988) found that the post-thinning reduction in interception with respect to control-plot values was 30.2% after one year, 25.8% after two years, 15.1% after four years, and subsequently close to zero. Similarly, Bréda et al. (1995) obtained values of 30.4% after one year and 0% after two years (though the authors themselves point out that the low year-2 value was partially attributable to an 18% drop in LAI in the control plot).

The time period after which interception will return to control values undoubtedly depends on the species and on environmental conditions. This explains the highly variable results obtained in different studies. For example, Aussenac and Boulangeat (1980) found that evapotranspiration levels remained different (by 18%) from the control values four years after thinning. In the present study, performed nine years after thinning, LAI in the treatment-A and treatment-C plots were practically the same, so that it would be surprising if a relationship between interception and biomass removed had been maintained.

Finally, in most cases thinning is performed in a systematic manner: for example, a row of trees is removed (Aussenac et al., 1981; Aussenac and Granier, 1988), or the separation between trees is increased in regular fashion (for example, to 2, 4, 6 or 8 m) (Teklehaimanot and Jarvis, 1991; Teklehaimanot et al., 1991). In the present study, however, thinning had been done by removing dominated trees. With systematic thinning and after relatively short time periods, canopy storage capacity can be considered a property of individual trees that is unaffected by stand density and spacing, since there is typically a closely linear relationship between number of trees per hectare and canopy storage capacity (Teklehaimanot and Jarvis, 1991). This relationship will probably not exist after heterogeneous thinning, because the

reduction in stand density or basal area is not proportional to the reduction in LAI. The effects of thinning on interception will thus be difficult to predict as stand density is unrelated to LAI. whether because of heterogeneous thinning (e.g. selective removal of dominated trees). or the passage of time. or both.

The fact that interception losses are not correlated with stand density but are correlated with LAI has been noted by Aussenac (1975). who detected a relatively small reduction in interception (from 23.8 to 17.2%. i.e. a reduction of 27.7%) after thinning of an oakwood plot that involved removal of 70% of trees and a 28% reduction in LAI. However. Bréda et al. (1995) reported similar interception in thinned and control plots. despite the existence of differences in LAI. which the authors attributed to differences in canopy structure between the two plots. Within both plots. LAI was positively correlated with interception. Thus the within-plot spatial distribution of LAI is another factor to be taken into account.

5. Conclusions

Our results indicate that throughfall in Canary Islands pine forest is seasonal. with smaller amounts in summer. reflecting seasonal variation in rainfall and possibly in the height of the cloud ceiling. Throughfall in our plots was very high: 2.0 times the incident rainfall in the control plots. 2.2 times incident rainfall in the lightly thinned plots. and 1.8 times incident rainfall in the heavily thinned plots. One non-thinned plot with atypical topographic characteristics showed throughfall that was 2.8 times incident rainfall. A randomized block experimental design was used. but despite significant among-block variation in topographic characteristics there was no consistent pattern of variation among blocks in throughfall (whether considering the whole study period. or individual measurement intervals). By contrast. both canopy characteristics and throughfall varied significantly among treatments (light thinning. heavy thinning. control): specifically. mean throughfall was significantly higher in the lightly thinned plots than the heavily thinned plots in most intervals. and significantly higher in the control plots than the lightly thinned plots in some intervals. A similar pattern is observed when total throughfall over the year of study is considered.

There was no significant relationship between topographic variables and total throughfall. However. total throughfall was significantly affected by basal area. LAI and tree height variability. and since all these variables varied significantly among treatments. they can be considered responsible for the observed among-treatment variation in throughfall. We found two different processes: (a) the lack of a proportional relationship between basal area removed and degree of increase in throughfall is caused by the long period (9 years) elapsed between thinning and throughfall measurement. and the lack of proportionality between BA and LAI (attributable to a heterogeneous thinning applied) and (b) the discrepancy between our results and those of previous studies. attributable to the importance of fog precipitation in our study area.

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