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Facultat de Biologia

**ESTRUCTURA I CONTINGUT DE NUTRIENTS A LES CAPÇADES DE
Quercus ilex L. DEL BOSC DE LES MUNTANYES DE PRADES:
INFLUÈNCIA DE LES CONDICIONS NATURALS DE CREIXEMENT I
EFECTE DE MANIPULACIONS EXPERIMENTALS**

**CANOPY STRUCTURE AND NUTRIENT CONTENT IN A *Quercus ilex* L.
FOREST OF PRADES MOUNTAINS: EFFECT OF NATURAL AND
EXPERIMENTAL MANIPULATION OF GROWTH CONDITIONS**

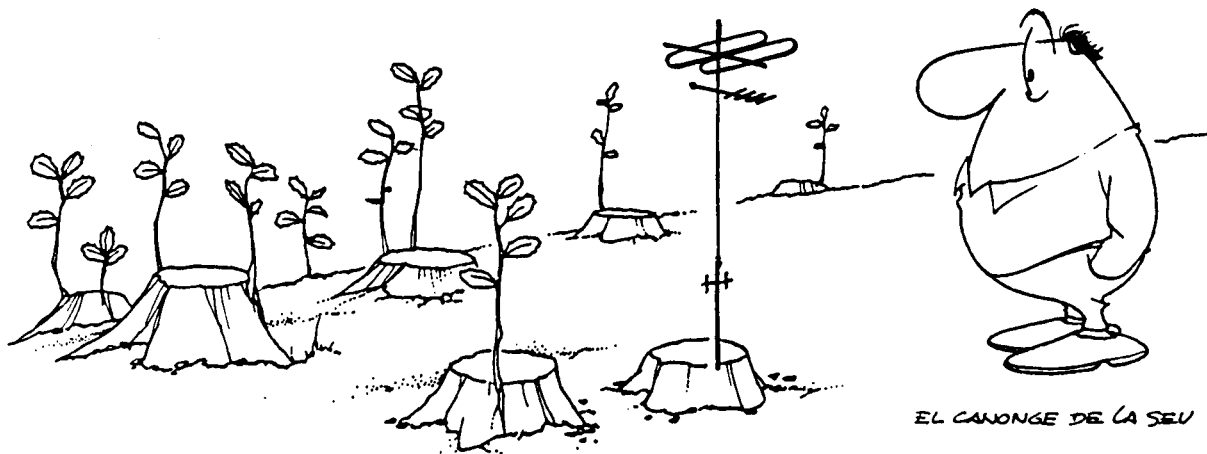
Santi Sabaté i Jorba

1993

5. Resposta de l'alzina al foc i a la tallada arreu

5.2. Contingut i dinàmica dels nutrients als rebrots d'alzina:

Effects of clearcutting and fire on Quercus ilex L. II. Nutrient content and resorption in the regenerating canopy



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5.2.1 Summary

Disturbances such as fire or clearcutting produce net losses of nutrients as well as a reorganization of nutrient pools available to plants. Holm oak (*Quercus ilex*) possess adaptative traits to survive or easily regenerate after disturbance. In order to compare the short-term effects of forest fire and clearcutting on a holm-oak forest, a disturbance experiment was designed. The study was carried out at the Prades Experimental Complex of Catchments. This holm-oak forest was managed until 1950's as a source of charcoal resulting in a multistemmed structure in the above ground biomass. In August 1988 two 40mx20m contiguous plots were clearcut. The logs and branches greater than 2 cm in diameter were removed but the slash was homogeneously distributed on the plots. In order to burn the slash a firebreak was established around one plot where all the aboveground biomass was removed. This plot was burned in October 1988. This study analyses and compares the nutrient content in *Quercus ilex* resprouts and the importance of nutrient variation in their canopy structures during the early regeneration phase (two years after disturbance), as well as nutrient resorption after (1) burning, (2) clearcutting and leaving the slash or (3) clearcutting and removing the slash (firebreak area). The nutrient content of resprouts were compared with those of terminal branches in the undisturbed forest. Regeneration of *Quercus ilex* occurred after each disturbance treatment. Differences with the undisturbed forest decreased with time. Minimum N, P, and S concentrations were found in summers. N and P mass variations (on leaf area basis) showed the importance of resorption supporting the idea of source-sink effect on resorption. Differences between treatments were a lower N concentration in the burned plot, lower initial importance of N mass resorption in the clearcut plot (with slash) and lower K concentration in firebreak area in concordance with a lower growth on the main axis (Sabaté and Gracia, unpublished manuscript, chapter 5.1.1).

5.2.2. Introduction

Disturbances such as fire or clearcutting produce changes in soil moisture and net losses of nutrients as well as a reorganization of nutrient pools which modifies their availability to plants (Raison 1979, Sollins et al. 1981, Christensen 1987). In Mediterranean regions, the forests have a long history of disturbance including wood extraction, charcoal production and fires that in the last few decades have been increased by man.

Quercus ilex forests offer a good example, being managed for firewood or charcoal production and sometimes affected by forest fires. Both disturbances kill the above ground parts and the trees usually regenerate by resprouting. Each of these disturbances removes a large amount of nutrients. Nevertheless, following repeated disturbances individual trees develop massive root crowns (lignotubers or burls) resulting a large root system (James 1984), frequently larger than the above ground biomass (Canadell and Rodà 1991).

Root crown systems could be important to nutrient and carbohydrate storage. These nutrients, as well as the new nutrient uptake, may support canopy re-growth. Nutrient resorption could be also important. It increases the possibility to re-use nutrients several times, and thus it increases nutrient use efficiency (Vitousek 1982) and it decreases external nutrient dependences. Ryan and Bormann (1982) found that the same amounts of N and P were resorbed comparing 5- and 55-year-old northern hardwood forests, indicating that the nutrient resorption mass is rapidly reestablished after its elimination by clearcutting related to the redevelopment of leaf biomass. As these forests, *Q. ilex* seems to have the same capacity in recovering leaf biomass (see Rapp et al. 1992, Sabaté and Gracia see chapter 5.1). So resorption may be a key factor in a rapid growth in height of the early successional steps acting as a conservative mechanism and reducing production costs (see Chapin 1989). Nambiar and Fife (1987) pointed out that the presence of actively growing needles serve as a sink for nutrient translocation in *Pinus radiata*. Chapin and Moilanen (1991) concluded that source-sink relationships did strongly influence efficiency of N and P resorption (see also Pugnaire and Chapin 1992).

In a nutrient cycling study of an undisturbed holm oak forest, Escarré et al. (1987) estimated that an important amount of N (48%) was used in new structures from other fractions (18% and 17% from one year old and senescing leaves, and 12% from branches). Also, 31% of P used in new structures was retranslocated (14% from one year old leaves and 17% from senescig leaves). These results suggested that leaves could act repeatedly as N and P retranslocation sources as did branches for N.

Recent studies based on *Q. ilex* foliar analysis and resorption from senescing leaves measured about 33% and 43% of N and P retranslocation (Mayor 1990, Mayor and Rodà 1992) but did not find good relationship between retranslocation and soil nutrient availability (see also Escudero et al. 1992a). On the other hand, Escudero et al. (1992a) found that leaf N concentrations did not decrease markedly during new flushes of shoot growth, so only once, about 30% of the maximum N pool from senescing leaves was retranslocated, contradicting the above suggestion. They basically argued that *Q. ilex* presents a very long period of leaf abscission as an adaptation to unpredictable water stress, and that length of leaf abscission affects negatively the retranslocation intensity (see also Del Arco et al. 1991). However, this generally does not decrease nutrient use efficiency because leaf longevity in evergreens could be more important in increasing retention time of nutrients than resorption from senescing leaves (Escudero et al. 1992b), so giving other possible advantages to evergreens (see Monk 1966) and explaining the correlation between nutrient status and leaf longevity (Jonasson 1989).

In a complementary paper (Sabaté and Gracia unpublished manuscript, see chapter 5.1) we showed the structural characteristics of canopy regeneration after fire and clearcutting in a holm oak forest. In this study we analyse and compare the nutrient content in *Quercus ilex* resprouts and the importance of nutrient variation in their canopy structures as well as nutrient resorption after (1) burning, (2) clearcutting and leaving the slash or (3) clearcutting without the slash (firebreak area). In addition we compare the nutrient content of resprouts with those of terminal branches in the undisturbed forest.

How canopy regrowth is established is important to understand the relative quick recovery of resprouters after different disturbances. The unbalanced above:underground biomass ratio affects the properties of the new canopy components and growth patterns. Nutrient content and structural characteristics of these components could be related to growth activity. Nutrient resorption could play an important role acting as conservative mechanism and enhancing new growth. The three compared situations (burning, clearcutting with slash and firebreak) could act differently since the amount and characteristics of nutrients and organic matter which remain on site are different. In addition, when forest is clearcut and slash is leaved on the site, it increases fire danger since dry mediterranean summers. On the other hand, if all slash matter is removed then cost increases as well as nutrient site impoverishment (canopy structures have an important amount of nutrients) and erosion danger. Finally, fire cause nutrient losses (volatilization, smoke and ashes outputs, etc) and erosion danger, but in addition a thermic impact on individuals.

5.2.3. Study area and methods

Detailed information about the site and the disturbance experiment are presented in the complementary paper about resprouts structural characteristics (Sabaté and Gracia in press). Essentials are reproduced here.

Study site

The study was carried out in a holm-oak forest at the Prades Experimental Complex of Catchments (NE Spain). The experimental plots are located on a steep slope (28°) oriented SSE (41° 21' N, 1° 01' E, 920 m elevation). The main rock type in the area is schist and the soils are Lithic and Typic Xerochrepts (USDA Soil Taxonomy, 1975) (Serrasolsas et al. 1991). The forest is a holm-oak coppice that was managed until the 1950's as a source of charcoal, resulted in a multistemmed structure in the aboveground biomass (now about 40 to 50 years old and 6 m height) and an older root system corresponding to the initial seedling trees of unknown age.

The disturbance experiment

In August 1988 two 40 m x 20 m contiguous plots were clearcut. The logs and branches greater than 2 cm in diameter were removed but the slash was homogeneously distributed on the plots giving a depth of about 0.5 m. In order to burn the slash on one plot, a firebreak area was formed by removing all the aboveground biomass and placing it on the plot to be burnt. The plot was burnt in October 1988. To compare the disturbance treatments with the undisturbed *Q. ilex* trees, three replicate control plots (8 m x 8 m) were situated in a contiguous area. Hence, after disturbance we considered three different initial situations for *Q. ilex* regeneration: (1) burned plot, (2) clearcut plot and (3) firebreak plot.

Sampling procedure and measurements

Despite no replicates of disturbed areas were available due to logistics problems and the large impact of these experiments, the same history and initial homogeneous characteristics of our disturbed area provide us the possibility to compare the effect of the different disturbance treatments on canopy regrowth at individuals level. Thus, in each plot three different root crowns were randomly selected at each collection date and several dominant resprouts were collected from each root crown. Samples were collected in late spring 1989 (sp89), summer (sm89), late autumn 1989 (au89), spring 1990 (sp90) and summer 1990 (sm90). Dominant resprouts were selected as representative of the possible future dominant

stems. In addition, three dominant branches were collected from different root crowns of each control plot.

The samples were taken to the laboratory and separated for each root crown into leaves and stems of different axis position. Leaves-1 and Stems-1 for the main axis, Leaves-2 and Stems-2 for second axis, Leaves-3 and Stems-3 for third axis, etc. On each axis was too difficult to separate in different flushes origin, so only clear immature shoots, where leaves had not been clearly expanded, were considered separately. Control samples were separated into leaves and stems of different ages. Carbon and nitrogen content were analysed for each fraction using a Carlo-Erba D-700 elemental analyzer. Phosphorus, potassium, calcium, magnesium and sulphur were analyzed using wet digestion and ICP-AES determination (Mateo and Sabaté, 1993, see chapter 2).

To obtain measurements on dry mass the samples were oven-dried at 70°C for 48h and the nutrient mass on leaf area basis ($\mu\text{g}/\text{cm}^2$) were estimated using the specific leaf weight measured on each leaf sample (Sabaté and Gracia unpublished manuscript, see chapter 5.1.). In summer 1990 leaf litterfall samples were collected below the canopy of each, root crown, and structural measurements (as mean area) indicated its origin was from Leaves-1 (unshowed data).

Retranslocation was referred to the nutrient mass on leaf area and defined as the positive difference between two sampling dates succeeded in time. Considering the independence between means obtained at each sampling date, the values were obtained as:

$$[\text{First nutrient mass} - \text{Second nutrient mass}] \pm [(\text{SD of first nutrient mass})^2 + (\text{SD of second nutrient mass})^2]^{1/2}$$

The mean percentage of nutrient mass retranslocation was calculated by the following equation:

$$100 \times [\text{First nutrient mass } (\mu\text{g cm}^{-2}) - \text{Second nutrient mass } (\mu\text{g cm}^{-2})] / \text{First nutrient mass } (\mu\text{g cm}^{-2})$$

This retranslocation calculation is similar to the resorption defined by other authors (see e.g. Chapin and Kedrowsky 1983, Shaver and Melillo 1984, Lajtha 1987, Lajtha and Klein 1988, Escudero et al. 1992ab, Pugnaire and Chapin, 1992), but we considered more than one possible retranslocation period as Nambiar and Fife (1987), not only resorption from senescing leaves.

Statistical analysis

Data were analysed using the SAS GLM procedure (SAS 1988) for a complete two-factor factorial model with disturbance treatment (PLOT) and sampling date (DATE) as main effects. On the other hand, comparisons of dependent variables among control and disturbed plots were made for each disturbed plot in autumn 1989 and summer 1990 with leaves or stems origin as main factor. Multiple comparisons among means were made using Least Significant Difference if the ANOVA F test revealed significant differences.

5.2.4. Results and Discussion

Nutrient content in leaves and stems

The nutrient contents in leaves are shown in Figure 5.2.1 (Leaves-1,-2, -3) and Table 5.2.1 (Leaves-4 and -5). Carbon values showed an initial slight increase with time until autumn 1989 in Leaves-1 and -2, then similar values after au89. The firebreak plot tended to show a slightly higher C concentration than the other treatments ($P < 0.01$ in Leaves-2), particularly than the burned plot ($P < 0.05$ in Leaves-3). Leaves-4 and -5 did not show differences between plots. The C concentrations in stems (Figure 5.2.2 and Table 5.2.2) were not significantly different between plots but some significant variation occurred over time. A higher C concentration was measured in autumn 1989 for Stems-1, -2 and -3 (Figure 5.2.2), probably as consequence of a relative carbohydrate increase. This is compatible with the high soluble carbohydrates in leaves measured in autumn a year later (autumn 1990) in the burned and clearcut plot by Fleck et al. (1993).

N, P and S concentrations in leaves showed a broadly similar pattern over time (Figure 5.2.1). These nutrients had high initial concentrations after disturbance, declining in sm89 then increasing to au89 and sp90, before declining again in sm90 to values comparable with the previous summer (sm89). The same nutrients in stems showed a similar pattern (Figure 5.2.2), however the concentration increase was not as pronounced as the observed for leaves. The N concentrations in au89 was as low as in sm89. P concentration was even lower in au89 than sm89 (significantly different for Stems-3, $P < 0.01$). These concentrations could reflect a dilution effect by the autumn increases of stem carbohydrates. K tended to decrease with time in Leaves-1 and -2 showing initial higher values (sp89 and sm89) until stabilising at a lower level after sm89. The K concentration in stems followed a similar pattern to leaves, but from higher initial values. Ca concentration tended to increase with time, but was only statistically significant for leaves and stems from the second-order axes ($P < 0.001$) (Figures 5.2.1 and 5.2.2).

There were some significant differences between treatments for N, P, K, Ca and S concentrations for both leaves and stems. N concentrations were generally lower on the burned plot (Figures and Tables 5.2.1 and 5.2.2). This could be due to N volatilization during the fire. P concentration was initially highest in Leaves-2 from the clearcut plot and lowest for burned plots. However, treatment differences dissipated after sp89 (Figures 5.2.1 and 5.2.2). K concentrations were generally lower in the firebreak plot possibly due to the removal of all above ground biomass. This is in agreement with the growth reduction observed on the firebreak plot (Sabaté and Gracia unpublished manuscript, see chapter 5.1). The higher values of C concentration mentioned above for this plot may reflect a nutrient

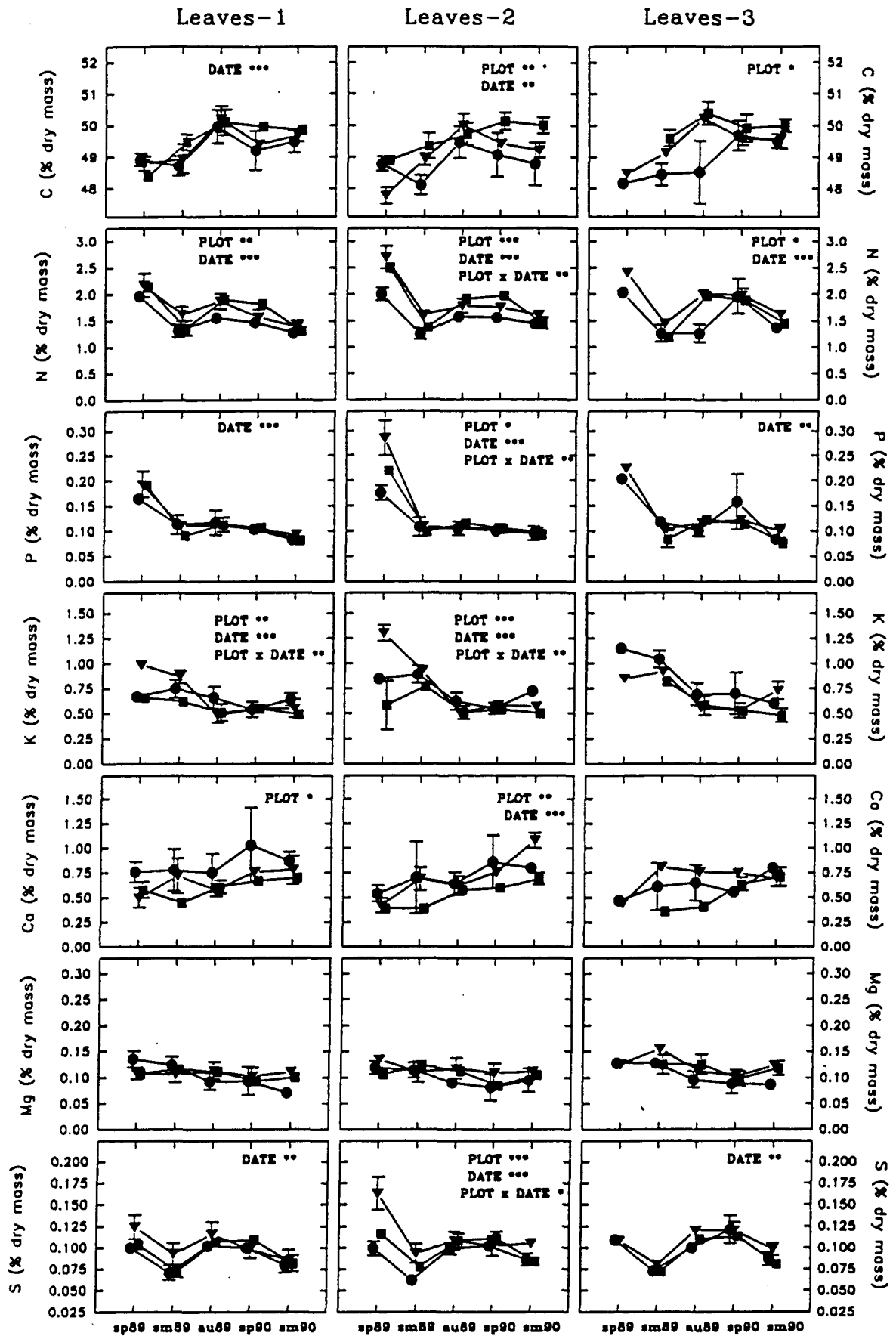
limitation and delaying of carbon allocation for new growth. Differences in K concentration were not significant for the leaves on the fourth and fifth axis, both produced mainly in summer 1990. S concentrations were initially significantly higher on the clearcut plot, but later on all treatments had similar values. There were no differences over time or between treatments for Mg concentrations.

Captions of Figures 5.2.1 and 5.2.2

Figure 5.2.1. Seasonal pattern of C, N, P, K, Ca, Mg and S concentrations for Leaves-1, -2 and -3. Significant differences between plots, sampling dates or interaction indicated by *, ** and *** at $P < 0.05$, $P < 0.01$ and $P < 0.001$ respectively. Data are means \pm SE, $n=3$ (three root crowns). For Leaves-3 $n=2$ in sp89 and sm89 on the burned plot, $n=1$ in sm89 and au89 in the clearcut plot, and $n=2$ in sp89 and sm90. SE is not shown if smaller than symbol. (sp=spring, sm=summer, au=autumn; first, second and third axes represented by -1, -2, and -3 respectively).

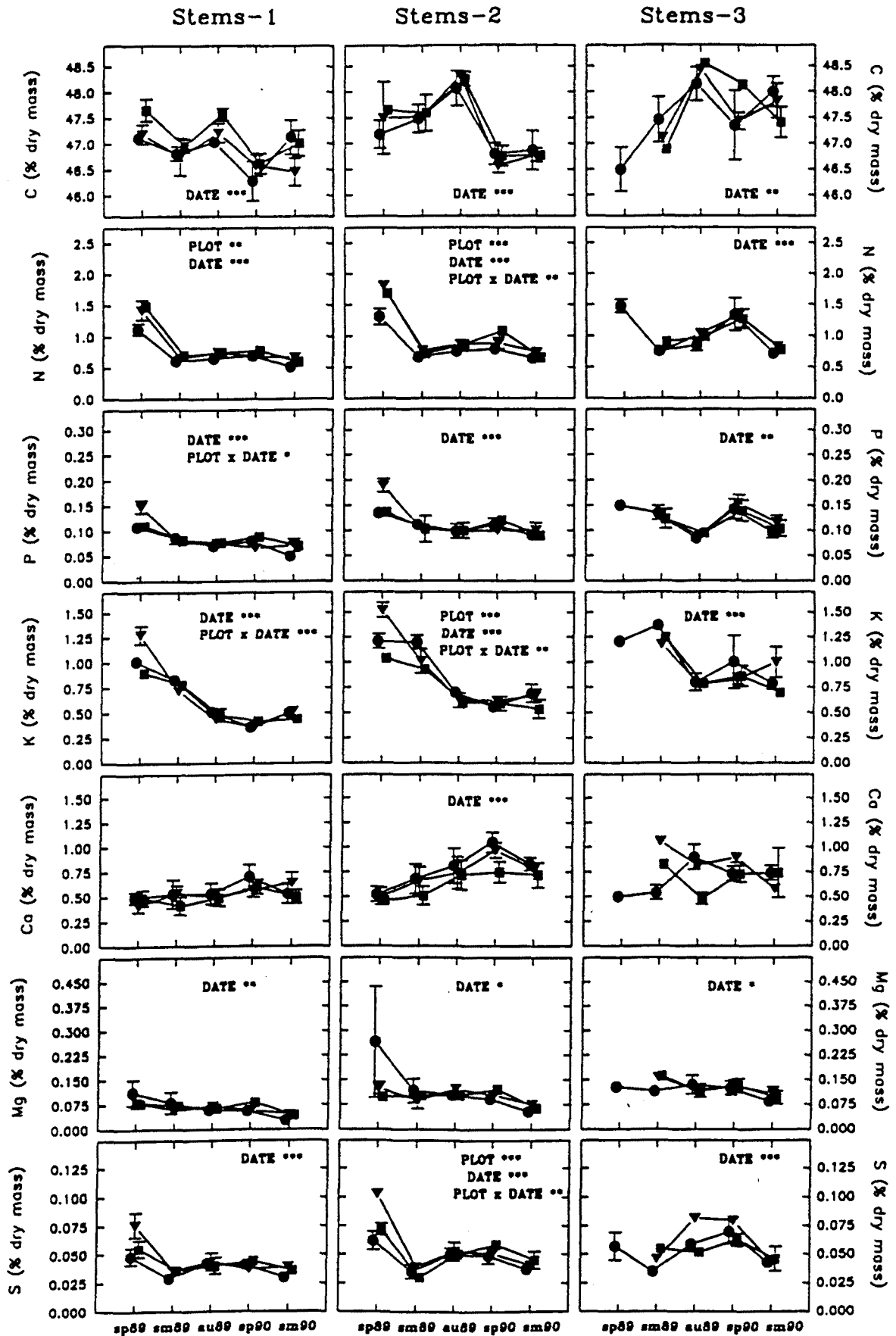
Figure 5.2.2. Seasonal pattern of C, N, P, K, Ca, Mg and S concentrations for Stems-1, -2 and -3. Significant differences between plots, sampling dates or interaction indicated by *, ** and *** at $P < 0.05$, $P < 0.01$ and $P < 0.001$ respectively. Data are means \pm SE, $n=3$ (three root crowns). For Stems-3 $n=2$ in sp89 and sm89 on the burned plot, $n=1$ in sm89 and au89 in the clearcut plot, and $n=2$ in sp89 and sm90. SE is not shown if smaller than symbol. (Symbols as in Figure 5.2.1).

Figure 5.2.1.



Burned plot ● , Clearcut plot ▼ , Firebreak plot ■

Figure 5.2.2.



Burned plot ● , Clearcut plot ▼ , Firebreak plot ■

Table 5.2.1. Mean C, N, P, K, Ca, Mg and S concentrations for Leaves-4 and -5. Data are means±SE, n=3 (root crowns). SE=, when n=1. For Leaves-5 n=2 on the clearcut and firebreak plots. Differences were not significant. (sp=spring, sm=summer, au=autumn).

	PLOT	Leaves-4				Leaves-5
		sm89	au89	sp90	sm90	sm90
C (% dry mass)	Burned	-	50.3± .	-	49.7±0.1	49.01±0.19
	Clearcut	48.8± .	49.0± .	49.4± .	49.4±0.2	49.23±0.22
	Firebreak	-	-	-	49.5±0.3	49.46±0.34
N (% dry mass)	Burned	-	1.66± .	-	1.41±0.12	1.28±0.09
	Clearcut	1.66± .	1.90± .	1.96± .	1.61±0.06	1.46±0.01
	Firebreak	-	-	-	1.47±0.04	1.61±0.07
P (% dry mass)	Burned	-	0.127± .	-	0.077±0.010	0.086±0.005
	Clearcut	0.117± .	0.144± .	0.123± .	0.103±0.011	0.096±0.007
	Firebrak	-	-	-	0.098±0.009	0.105±0.005
K (% dry mass)	Burned	-	0.96± .	-	0.70±0.05	0.81±0.03
	Clearcut	0.93± .	0.76± .	0.61± .	0.85±0.09	0.80±0.01
	Firebreak	-	-	-	0.72±0.05	0.70±0.07
Ca (% dry mass)	Burned	-	0.61± .	-	0.55±0.04	0.40±0.07
	Clearcut	0.51± .	0.30± .	0.69± .	0.53±0.09	0.39±0.02
	Firebreak	-	-	-	0.40±0.06	0.42±0.02
Mg (% dry mass)	Burned	-	0.097± .	-	0.094±0.010	0.103±0.012
	Clearcut	0.129± .	0.174± .	0.107± .	0.112±0.007	0.112±0.005
	Firebreak	-	-	-	0.106±0.004	0.108±0.012
S (% dry mass)	Burned	-	0.136± .	-	0.082±0.005	0.077±0.003
	Clearcut	0.098± .	0.441± .	0.115± .	0.088±0.009	0.082±0.002
	Firebreak	-	-	-	0.078±0.002	0.084±0.009

Table 5.2.2. Mean C, N, P, K, Ca, Mg and S concentrations for Stems-4 and -5. Data are means \pm SE, n=3 (root crowns). SE=, when n=1. For Stems-5 n=2 on the clearcut and firebreak plots. Differences were not significant. (sp=spring, sm=summer, au=autumn; fourth and fifth axes represented by -4 and -5 respectively).

	PLOT	Stems-4				Stems-5
		sm89	au89	sp90	sm90	sm90
C (% dry mass)	Burned	-	48.7 \pm .	-	48.0 \pm 0.4	48.2 \pm 0.2
	Clearcut	47.1 \pm .	47.9 \pm .	47.5 \pm .	48.1 \pm 0.1	47.6 \pm 0.2
	Firebreak	-	-	-	48.5 \pm 0.1	47.6 \pm .
N (% dry mass)	Burned	-	1.01 \pm .	-	0.82 \pm 0.02	0.82 \pm 0.05
	Clearcut	0.97 \pm .	1.17 \pm .	1.20 \pm .	1.04 \pm 0.04	0.88 \pm 0.05
	Firebreak	-	-	-	0.99 \pm 0.05	0.96 \pm .
P (% dry mass)	Burned	-	0.095 \pm .	-	0.092 \pm 0.010	0.089 \pm 0.009
	Clearcut	0.122 \pm .	0.105 \pm .	0.138 \pm .	0.137 \pm 0.020	0.097 \pm 0.003
	Firebreak	-	-	-	0.114 \pm 0.012	0.119 \pm .
K (% dry mass)	Burned	-	0.75 \pm .	-	1.07 \pm 0.13	0.92 \pm 0.05
	Clearcut	1.06 \pm .	0.58 \pm .	0.89 \pm .	1.32 \pm 0.06	1.16 \pm 0.03
	Firebreak	-	-	-	0.93 \pm 0.09	0.77 \pm .
Ca (% dry mass)	Burned	-	0.76 \pm .	-	0.72 \pm 0.12	0.58 \pm 0.01
	Clearcut	0.96 \pm .	0.77 \pm .	0.77 \pm .	0.51 \pm 0.05	0.52 \pm 0.05
	Firebreak	-	-	-	0.57 \pm 0.12	0.82 \pm .
Mg (% dry mass)	Burned	-	0.135 \pm .	-	0.108 \pm 0.005	0.116 \pm 0.006
	Clearcut	0.171 \pm .	0.099 \pm .	0.115 \pm .	0.122 \pm 0.011	0.129 \pm 0.008
	Firebreak	-	-	-	0.141 \pm 0.003	0.153 \pm .
S (% dry mass)	Burned	-	0.066 \pm .	-	0.050 \pm 0.004	0.050 \pm 0.004
	Clearcut	0.053 \pm .	0.096 \pm .	0.065 \pm .	0.056 \pm 0.005	0.051 \pm 0.002
	Firebreak	-	-	-	0.060 \pm 0.003	0.077 \pm .

Structure of coppice regrowth compared to that of the undisturbed forest

The leaves and stem nutrient concentrations measured in autumn 1989 and summer 1990 for the undisturbed forest are shown in Table 5.2.3. The leaves had higher C, N and S concentration than stems, and lower P, K, Mg and Ca. This pattern in chemical composition is in agreement with Clemente (1983), working in the same forest, and other undisturbed holm oak forests (Ferrés 1984, Mayor 1990, Mayor and Rodà 1992, Canadell and Vila 1992). Compared to nutrient concentrations in leaves and stems of the resprouts produced after the disturbance treatments, the above pattern is similar to that of 4th- and 5th-order axes (Tables 5.2.1 and 5.2.2) but different to that of 1st-, 2nd- and 3rd-order axes.

The Leaves -1, 2 and 3 had higher C, N and S concentrations than stems, as the pattern showed above, but these leaves had as well higher Mg concentration. Leaves 1 had higher P and Ca concentration than stems and these were similar in leaves and stems for 2nd- and 3rd axes. Furthermore, K concentration in Leaves 1, 2 and 3 had similar values than stems (all of them lower above). This pattern observed in the disturbed forest basically agrees with the pattern showed by Rapp et al. (1992) in *Q. ilex* regeneration after clearcut. These higher nutrient concentrations observed in leaves is accord with their high production capacity during the first regeneration steps, as reflected by their higher photosynthetic and transpiration rates (Castell 1992, Fleck et al. 1993) and the rapid canopy re-growth (Sabaté and Gracia unpublished manuscript, see chapter 5.1). This also agrees with the positive relationship between leaf N concentration and photosynthesis showed by several authors (Field and Mooney 1986, Lajtha and Whitford 1989, Evans 1989 and Reich et al. 1992).

The N and P concentration comparisons between different axes and values from the undisturbed plot were made for autumn 1989 and summer 1990. These results are showed in the Tables 5.2.6 and 5.2.7 for autumn 1989 and Tables 5.2.8 and 5.2.9 for summer 1990 (leaves&stems respectively). Both sampling dates were chosen to contrast with the higher (in autumn) and lower (in summer) concentration values obtained from the disturbed plots.

In autumn 1989 the differences between the P and N concentration in leaves were lower in the burned plot than in the others treatment plots (Table 5.2.6). In this plot, no significant differences in P concentration were found and N was lower in leaves from the third axis and the oldest leaves from undisturbed plot (Leaves-87). The small differences noted before in the burned plot is related to the general lower N concentration in that plot, that got closer values to the undisturbed plot than the other treatments. The axes presented similar values in the clearcut and firebreak plots, but N concentrations were higher than in the undisturbed plots.

The differences in phosphorus appeared only for older leaves that had, as with N,

lower P concentrations. Dissimilarity between N concentrations in stems showed in Table 5.2.7 are due to the higher values on stems from undisturbed plots specially on stems-89. The contrasts were larger in the burned plot because had lower N concentrations than the other plots. Scarce differences in P concentrations were found, only significant after lower values on stems-1 and higher values on stems-89.

In summer 1990, differences in leaf N concentrations on the burned plot were not significant between axis, neither to the control plots (Table 5.2.8). The clearcut plot presented higher leaf N concentrations than the control plots, only Leaves-1 had lower values then closer to the control plots. The firebreak plot showed few differences to the control plots, only for leaves-89 with lower N concentration values.

Differences in P concentrations were due to the higher values on younger leaves from the control plots. These contrasts were fewer on the clearcut plot after closer leaf P concentrations values on the third, fourth and fifth axes to the leaves from the control plots produced in spring 1990. The comparisons between stems are shown in Table 5.2.9. A similar pattern in stem N concentrations presented all disturbance treatments. The lower stem N concentrations on the first and second axes is a general characteristic. However, the common lower N concentrations in the burned plot increased differences compared to those showed on the clearcut and the firebreak plots, where the fourth and fifth axes did not differ to the controls. P concentrations were higher on stems from the control plots. The lowest values appeared on the main axis and the highest on the Stems-89. These differences were pronounced in the burned plot where also the Stems-88 and Stems-90 P concentrations differed to the other stems.

Table 5.2.3. Mean leaves and stems C, N, P, K, Ca, Mg and S concentrations on the control plots. Leaves and stems produced in spring 87,88,89 and 90. Samples collected in autumn 1988 (au88) and summer 1990 (sm90). Data are means \pm SE, n=9.

	Leaves-87		Leaves-88		Leaves-89		Leaves-90
SAMPLING DATE	au89	au89	sm90	au89	sm90	sm90	
C (% D.W.)	50.5 \pm 0.1	50.5 \pm 0.2	49.9 \pm 0.2	51.2 \pm 0.3	48.9 \pm 0.3	49.4 \pm 0.2	
N (% D.W.)	1.34 \pm 0.02	1.55 \pm 0.05	1.31 \pm 0.04	1.46 \pm 0.01	1.13 \pm 0.03	1.35 \pm 0.05	
P (% D.W.)	0.081 \pm 0.005	0.085 \pm 0.004	0.074 \pm 0.005	0.091 \pm 0.006	0.148 \pm 0.017	0.124 \pm 0.006	
K (% D.W.)	0.41 \pm 0.02	0.46 \pm 0.03	0.56 \pm 0.02	0.44 \pm 0.03	1.18 \pm 0.02	0.96 \pm 0.04	
Ca (% D.W.)	0.79 \pm 0.04	0.84 \pm 0.07	0.89 \pm 0.05	0.59 \pm 0.10	0.77 \pm 0.00	0.31 \pm 0.02	
Mg (% D.W.)	0.050 \pm 0.004	0.063 \pm 0.004	0.079 \pm 0.005	0.087 \pm 0.001	0.217 \pm 0.000	0.116 \pm 0.008	
S (% D.W.)	0.106 \pm 0.007	0.105 \pm 0.005	0.110 \pm 0.003	0.094 \pm 0.004	0.147 \pm 0.000	0.107 \pm 0.005	
	Stems-87		Stems-88		Stems-89		Stems-90
SAMPLING DATE	au89	au89	sm90	au89	sm 90	sm90	
C (% D.W.)	48.3 \pm 0.2	46.4 \pm 0.2	47.8 \pm 0.2	48.7 \pm 0.3	49.4 \pm 0.2	48.2 \pm 0.2	
N (% D.W.)	0.99 \pm 0.02	1.00 \pm 0.05	1.01 \pm 0.03	1.27 \pm 0.03	0.96 \pm 0.05	0.97 \pm 0.04	
P (% D.W.)	0.107 \pm 0.006	0.098 \pm 0.006	0.142 \pm 0.014	0.145 \pm 0.012	0.209 \pm 0.023	0.138 \pm 0.010	
K (% D.W.)	0.44 \pm 0.02	0.50 \pm 0.02	0.75 \pm 0.03	0.74 \pm 0.07	1.27 \pm 0.006	1.12 \pm 0.05	
Ca (% D.W.)	1.26 \pm 0.08	1.09 \pm 0.12	1.21 \pm 0.08	0.89 \pm 0.05	0.91 \pm 0.05	0.70 \pm 0.07	
Mg (% D.W.)	0.079 \pm 0.005	0.091 \pm 0.006	0.118 \pm 0.011	0.123 \pm 0.016	0.156 \pm 0.010	0.224 \pm 0.096	
S (% D.W.)	0.073 \pm 0.002	0.077 \pm 0.004	0.088 \pm 0.003	0.118 \pm 0.024	0.186 \pm 0.047	0.093 \pm 0.009	

Captions of Tables 5.2.6, 5.2.7, 5.2.8 and 5.2.9

Table 5.2.6. Multiple comparisons of mean P (above diagonal matrix) and N (below diagonal matrix) concentrations for leaves from different axes and control plots (produced in spring 87, 88 and 89) to each disturbance treatment. Values from autumn 1989. ANOVA probability in parenthesis. Significant differences between mean values indicated by n.s. (no significant), *, ** and *** at $P < 0.05$, $P < 0.01$ and $P < 0.001$ respectively (LSD test).

Table 5.2.7. Multiple comparisons of mean P (above diagonal matrix) and N (below diagonal matrix) concentrations for stems from different axes and control plots (produced in spring 87, 88 and 89) to each disturbance treatment. Values from autumn 1989. ANOVA probability in parenthesis. Significant differences as in Table 5.2.6.

Table 5.2.8. Multiple comparisons of mean P (above diagonal matrix) and N (below diagonal matrix) concentrations for leaves from different axes and control plots (produced in spring 88, 89 and 90) to each disturbance treatment. Values from summer 1990. ANOVA probability in parenthesis. Significant differences as in table 5.2.6.

Table 5.2.9. Multiple comparisons of mean P (above diagonal matrix) and N (below diagonal matrix) concentrations for stems from different axes and control plots (produced in spring 88, 89 and 90) to each disturbance treatment. Values from summer 1990. ANOVA probability in parenthesis. Significant differences as in table 5.2.6.

Table 5.2.6.

PHOSPHORUS (P<0.1568)						
SAMPLING DATE au89	BURNED PLOT			CONTROL PLOT		
	Leaves-1	Leaves-2	Leaves-3	Leaves-87	Leaves-88	Leaves-89
Leaves-1	----
Leaves-2	n.s.	----
Leaves-3	*	*	----	.	.	.
Leaves-87	*	*	n.s.	----	.	.
Leaves-88	n.s.	n.s.	**	*	----	.
Leaves-89	n.s.	n.s.	n.s.	n.s.	n.s.	----
NITROGEN (P<0.0246)						
PHOSPHORUS (P<0.0084)						
SAMPLING DATE au89	CLEARCUT PLOT			CONTROL PLOT		
	Leaves-1	Leaves-2	Leaves-3	Leaves-87	Leaves-88	Leaves-89
Leaves-1	----	n.s.	n.s.	*	*	n.s.
Leaves-2	n.s.	----	n.s.	*	n.s.	n.s.
Leaves-3	n.s.	n.s.	----	*	n.s.	n.s.
Leaves-87	***	***	***	----	n.s.	n.s.
Leaves-88	**	*	*	*	----	n.s.
Leaves-89	**	*	**	n.s.	n.s.	----
NITROGEN (P<0.0005)						
PHOSPHORUS (P<0.0108)						
SAMPLING DATE au89	FIREBREAK PLOT			CONTROL PLOT		
	Leaves-1	Leaves-2	Leaves-3	Leaves-87	Leaves-88	Leaves-89
Leaves-1	----	n.s.	n.s.	*	*	n.s.
Leaves-2	n.s.	----	n.s.	**	*	n.s.
Leaves-3	n.s.	n.s.	----	**	**	n.s.
Leaves-87	***	***	***	----	n.s.	n.s.
Leaves-88	***	***	***	**	----	n.s.
Leaves-89	***	***	***	n.s.	n.s.	----
NITROGEN (P<0.0001)						

Table 5.2.7.

PHOSPHORUS ($P < 0.0098$)						
SAMPLING DATE au89	BURNED PLOT			CONTROL PLOT		
	Stems-1	Stems-2	Stems-3	Stems-87	Stems-88	Stems-89
Stems-1	----	n.s.	n.s.	*	*	***
Stems-2	n.s.	----	n.s.	n.s.	n.s.	*
Stems-3	n.s.	n.s.	----	n.s.	n.s.	**
Stems-87	***	**	n.s.	----	n.s.	*
Stems-88	***	**	n.s.	n.s.	----	**
Stems-89	***	***	**	**	**	----

NITROGEN ($P < 0.0001$)

PHOSPHORUS ($P < 0.0213$)						
SAMPLING DATE au89	CLEARCUT PLOT			CONTROL PLOT		
	Stems-1	Stems-2	Stems-3	Stems-87	Stems-88	Stems-89
Stems-1	----	n.s.	n.s.	*	n.s.	***
Stems-2	n.s.	----	n.s.	n.s.	n.s.	*
Stems-3	n.s.	n.s.	----	n.s.	n.s.	*
Stems-87	*	n.s.	n.s.	----	n.s.	*
Stems-88	**	n.s.	n.s.	n.s.	----	**
Stems-89	***	**	n.s.	**	**	----

NITROGEN ($P < 0.0028$)

PHOSPHORUS ($P < 0.0174$)						
SAMPLING DATE au89	FIREBREAK PLOT			CONTROL PLOT		
	Stems-1	Stems-2	Stems-3	Stems-87	Stems-88	Stems-89
Stems-1	----	n.s.	n.s.	n.s.	n.s.	**
Stems-2	n.s.	----	n.s.	n.s.	n.s.	*
Stems-3	*	n.s.	----	n.s.	n.s.	*
Stems-87	**	n.s.	n.s.	----	n.s.	*
Stems-88	**	n.s.	n.s.	n.s.	----	**
Stems-89	***	***	*	**	**	----

NITROGEN ($P < 0.0009$)

Table 5.2.8.

PHOSPHORUS (P<0.0001)								
SAMPLING DATE sm90	BURNED PLOT					CONTROL PLOT		
	Leaves-1	Leaves-2	Leaves-3	Leaves-4	Leaves-5	Leaves-88	Leaves-89	Leaves-90
Leaves-1	----	n.s.	n.s.	n.s.	n.s.	n.s.	***	**
Leaves-2	.	----	n.s.	n.s.	n.s.	n.s.	**	*
Leaves-3	.	.	----	n.s.	n.s.	n.s.	***	**
Leaves-4	.	.	.	----	n.s.	n.s.	***	***
Leaves-5	----	n.s.	**	**
Leaves-88	----	***	***
Leaves-89	----	n.s.
Leaves-90	----
NITROGEN (P<0.2496)								
PHOSPHORUS (P<0.0003)								
SAMPLING DATE sm90	CLEARCUT PLOT					CONTROL PLOT		
	Leaves-1	Leaves-2	Leaves-3	Leaves-4	Leaves-5	Leaves-88	Leaves-89	Leaves-90
Leaves-1	----	n.s.	n.s.	n.s.	n.s.	n.s.	**	*
Leaves-2	*	----	n.s.	n.s.	n.s.	n.s.	**	*
Leaves-3	*	n.s.	----	n.s.	n.s.	n.s.	**	n.s.
Leaves-4	*	n.s.	n.s.	----	n.s.	*	*	n.s.
Leaves-5	n.s.	n.s.	n.s.	n.s.	----	n.s.	**	n.s.
Leaves-88	n.s.	**	**	**	n.s.	----	***	***
Leaves-89	*	***	***	***	*	n.s.	----	n.s.
Leaves-90	n.s.	**	**	**	n.s.	n.s.	*	----
NITROGEN (P<0.0004)								
PHOSPHORUS (P<0.0001)								
SAMPLING DATE sm90	FIREBREAK PLOT					CONTROL PLOT		
	Leaves-1	Leaves-2	Leaves-3	Leaves-4	Leaves-5	Leaves-88	Leaves-89	Leaves-90
Leaves-1	----	n.s.	n.s.	n.s.	n.s.	n.s.	***	**
Leaves-2	n.s.	----	n.s.	n.s.	n.s.	n.s.	**	**
Leaves-3	n.s.	n.s.	----	n.s.	n.s.	n.s.	***	***
Leaves-4	n.s.	n.s.	n.s.	----	n.s.	n.s.	**	*
Leaves-5	*	n.s.	n.s.	n.s.	----	*	*	n.s.
Leaves-88	n.s.	n.s.	n.s.	n.s.	*	----	***	***
Leaves-89	n.s.	*	*	*	**	n.s.	----	n.s.
Leaves-90	n.s.	n.s.	n.s.	n.s.	*	n.s.	*	----
NITROGEN (P<0.0353)								

Table 5.2.9.

PHOSPHORUS (P<0.0001)								
SAMPLING DATE sm90	BURNED PLOT					CONTROL PLOT		
	Stems-1	Stems-2	Stems-3	Stems-4	Stems-5	Stems-88	Stems-89	Stems-90
Stems-1	---	n.s.	n.s.	n.s.	n.s.	***	***	***
Stems-2	n.s.	---	n.s.	n.s.	n.s.	*	***	*
Stems-3	**	n.s.	---	n.s.	n.s.	*	***	*
Stems-4	***	*	n.s.	---	n.s.	*	***	*
Stems-5	***	*	n.s.	n.s.	---	*	***	*
Stems-88	***	***	***	**	**	---	*	n.s.
Stems-89	***	***	**	n.s.	n.s.	n.s.	---	**
Stems-90	***	***	***	*	**	n.s.	n.s.	---

NITROGEN (P<0.0001)

PHOSPHORUS (P<0.0077)								
SAMPLING DATE sm90	CLEARCUT PLOT					CONTROL PLOT		
	Stems-1	Stems-2	Stems-3	Stems-4	Stems-5	Stems-88	Stems-89	Stems-90
Stems-1	---	n.s.	n.s.	*	n.s.	**	***	**
Stems-2	n.s.	---	n.s.	n.s.	n.s.	n.s.	**	n.s.
Stems-3	n.s.	n.s.	---	n.s.	n.s.	n.s.	**	n.s.
Stems-4	***	**	*	---	n.s.	n.s.	*	n.s.
Stems-5	*	n.s.	n.s.	n.s.	---	n.s.	**	n.s.
Stems-88	***	***	*	n.s.	n.s.	---	*	n.s.
Stems-89	**	*	n.s.	n.s.	n.s.	n.s.	---	*
Stems-90	***	**	n.s.	n.s.	n.s.	n.s.	n.s.	---

NITROGEN (P<0.0004)

PHOSPHORUS (P<0.0040)								
SAMPLING DATE sm90	FIREBREAK PLOT					CONTROL PLOT		
	Stems-1	Stems-2	Stems-3	Stems-4	Stems-5	Stems-88	Stems-89	Stems-90
Stems-1	---	n.s.	n.s.	n.s.	n.s.	**	***	**
Stems-2	n.s.	---	n.s.	n.s.	n.s.	*	***	*
Stems-3	*	n.s.	---	n.s.	n.s.	n.s.	**	n.s.
Stems-4	***	***	*	---	n.s.	n.s.	**	n.s.
Stems-5	**	**	n.s.	n.s.	---	n.s.	*	n.s.
Stems-88	***	***	**	n.s.	n.s.	---	*	n.s.
Stems-89	***	**	*	n.s.	n.s.	n.s.	---	*
Stems-90	***	***	**	n.s.	n.s.	n.s.	n.s.	---

NITROGEN (P<0.0001)

Nutrient mass variation and resorption on leaf area basis

The fluctuations in nutrient concentrations as N, P, K and S (Figures 5.2.1 and 5.2.2) could suggest possible nutrients movement or simply dilution effects (see Schlesinger et al. 1989, Escudero et al. 1992a). Figure 5.2.3 shows the N, P and K mass on leaf area basis and these results tended to reflect similar patterns than nutrient concentrations in leaves, in spite of possible dilution effects by increasing specific leaf weight (Sabaté and Gracia unpublished manuscript, see chapter 5.1). Significant differences over time were a general characteristic except for K in Leaves-1. These results suggest N and P retranslocation to the new growing structures in summer and replenishment in autumn-spring as found by Fife and Nambiar (1987) for *Pinus radiata*. Escarré et al. (1987) also suggested that *Q. ilex ssp ilex* leaves showed retranslocation processes repeatedly during its life-span, but Escudero et al. (1992a) did not find such pattern on *Q. ilex ssp rotundifolia* in drier areas.

In our experiment, with initial good regrowth conditions, an important source-sink effect takes place enhancing the importance of retranslocation. Leaves had a relative maximum K mass on leaf area basis in sm89 probably coincident with high transpiration values as measured on *Q. ilex* Castell (1992) in a clearcut experiment during the first year after disturbance, as measured also by Fleck (1993) measured during the second year at our experiment on the clearcut and burned plots.

Despite the differences in N mass on leaf area basis between plots not being significant for Leaves-1 and -2, generally the values on the burned plot were lower than values from the clearcut and firebreak plots. Another trait, showed by the clearcut plot, is the initial lower values on N mass on leaf area basis that did not present an initial relative maximum mass on leaf area basis as the burned and clearcut plots.

P mass on leaf area basis showed in the same plot an initial lower decrease between sp89 to sm89 than the other plots, despite the higher initial P concentrations. Both cases suggest a clear dilution effect of nutrient concentration values, that could be explained by the initial lower values of specific leaf weight due to the slash presence (Sabaté and Gracia, unpublished manuscript, see chapter 5.1). These leaves did not accumulate an initial N capital retranslocated later on as showed the burned and firebreak plots.

Table 5.2.4 shows the C, N, P and K concentrations and N, P and K mass on leaf area basis measured on leaf litterfall from Leaves-1 in summer 1990. In spite of differences between plots being not significant, leaf litter followed the same pattern than green leaves with lower N concentration and N mass on leaf area basis in the burned plot.

Table 5.2.4. Mean C, N, P and K concentrations and N, P and K mass on leaf area basis ($\mu\text{g}/\text{cm}^2$) measured on leaf litterfall from Leaves-1 in summer 1990. Data are means \pm SE, n=3.

Leaf litterfall from Leaves-1							
PLOT	(% dry mass)				($\mu\text{g} / \text{cm}^2$)		
	C	N	P	K	N	P	K
Burned	49.2 \pm 0.3	1.31 \pm 0.10	0.130 \pm 0.011	0.98 \pm 0.04	163.4 \pm 15.2	16.2 \pm 1.5	122.0 \pm 6.9
Clearcut	49.5 \pm 0.1	1.53 \pm 0.11	0.091 \pm 0.005	0.68 \pm 0.10	207.7 \pm 20.5	12.5 \pm 1.3	93.0 \pm 14.8
Firebreak	49.5 \pm 0.3	1.63 \pm 0.18	0.082 \pm 0.011	0.63 \pm 0.04	224.9 \pm 27.2	12.1 \pm 1.5	93.1 \pm 6.4

Table 5.2.5. Mean N and P mass resorption ($\mu\text{g}/\text{cm}^2$) and its percentage for Leaves-1 between different life-span periods (sp89-sm89 period, and au89 or sp89-sm90) and from leaf litterfall (au89 or sp90-leaf fall). Data are means \pm SE, n=3.

Leaves-1	PLOT	(sp89-sm89)		*(au89 or sp90)-(sm90)		*(au89 or sp90)-leaf litterfall	
		Mass	%	Mass	%	Mass	%
Mass N ($\mu\text{g}/\text{cm}^2$)	Burned	93.2 \pm 34.2	30.4	48.4 \pm 29.5	16.7	126.6 \pm 37.9	43.7
	Clearcut	0.4 \pm 104.3	0.2	86.5 \pm 61.2	24.3	147.9 \pm 52.9	41.6
	Firebreak	113.6 \pm 52.6	33.6	130.8 \pm 61.4	35.7	141.7 \pm 75.4	38.7
Mass P ($\mu\text{g}/\text{cm}^2$)	Burned	7.17 \pm 6.65	28.1	4.64 \pm 2.71	22.7	4.18 \pm 3.78	20.5
	Clearcut	5.64 \pm 11.21	24.9	2.21 \pm 4.34	11.0	7.61 \pm 4.12	37.8
	Firebreak	15.61 \pm 1.66	51.2	6.80 \pm 3.92	31.7	9.37 \pm 4.33	43.6

* The largest nutrient mass on leaf area basis.

The nutrient mass on leaf area basis were used to compute the N and P resorption from senescing leaves (leaf litterfall) showed in Table 5.2.5. The percentage values presented are similar to those showed by other authors for *Q. ilex*. Mayor and Rodà (1992) measured 33% of N and 43% of P retranslocation from senescing leaves. Escudero et al. (1992a) found lower N retranslocation values from senescing leaves (about 30%), but as we noted above their *Q. ilex* is another subspecies *Quercus ilex ssp rotundifolia* that growth under lower water availability conditions, with longer leaf-span and then probably more supporting leaf tissues (Chabot and Hicks 1982) than *Q. ilex ssp ilex* from our and the other studies mentioned. In addition of retranslocation from leaf fall, Table 5.2.5 shows other relatively important retranslocation processes except for clearcut plot that initially did not presents N withdrawal from Leaves-1 in the sp89-sm89 period as we remarked above (see Figure 5.2.3).

The nutrient use efficiency (NUE) concept has been developed and analysed by several authors taking into account nutrient concentrations in plant parts (e.g. Chapin 1980, 1988, Shaver and Melillo 1984), litterfall (Vitousek 1982, Birk and Vitousek 1986) or dynamics components as mean residence time of nutrient in the plant and the instantaneous rate of carbon fixation per unit of nutrient in the plant, as done Berendse and Aerts (1987) and Aerts (1990). These authors focus NUE at the whole plant level that is as interesting as difficult, especially with the large and complex root systems (see Canadell and Rodà 1991) prevailing under dry conditions.

The root crown systems provide nutrients and carbohydrates stored before disturbance to regrowth. How much is new nutrient uptake and production after disturbance (initial high transpiration and photosynthesis rates) or used from stored reserves is unknown in this study. The proportion of resources origin modifies the importance of dynamic components, e.g. high nutrient productivity and residence time is enhanced if is using mainly internal nutrient reserves. Given the initial homogeneity between individuals (same history and above ground biomass age) we assume no important initial differences in the mean level of stored reserves in individual stools before treatments.

Estimating the NUE as the inverse of nutrient concentration (Chapin 1980, 1988, Shaver and Melillo 1984). the burned plot showed a higher N use efficiency than the other treatment plots resulting from a lower N concentration but a higher or comparable growth (Sabaté and Gracia, unpublished manuscript, see chapter 5.1). A general lower N and P stems concentrations in sm90 (see Figure 5.2.2, Table 5.2.3 and Table 5.2.9) on the main, second and third axes, compared to the undisturbed plot with comparable age indicated that probably during regrowth these nutrients were used with higher efficiency. In relation to leaves the nutrient mass mobility and resorption once and again during its life-span enhance residence time of these nutrients increasing carbon gain per unit of available nutrient.

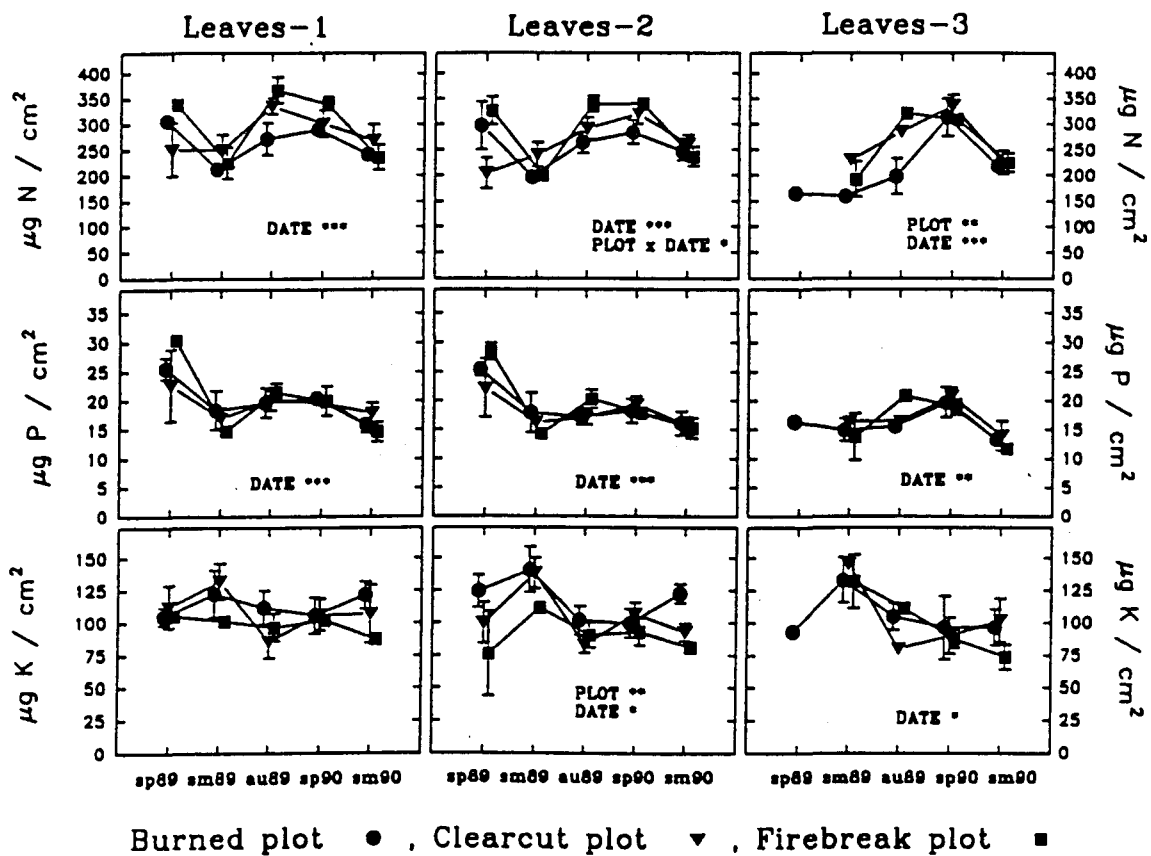


Figure 5.2.3. Seasonal pattern of N, P, and K nutrient mass variation on leaf area basis ($\mu\text{g}/\text{cm}^2$) for leaves-1, -2 and -3. Significant differences between plots, sampling dates or interaction indicated by *, ** and *** at $P < 0.05$, $P < 0.01$ and $P < 0.001$ respectively. Data are means \pm SE, $n=3$ (root crowns). For Leaves-3 $n=2$ in sp89 and sm89 on the burned plot, $n=1$ in sm89 and au89 on the clearcut plot, and $n=2$ in sp89 and sm90 on firebreak plot. SE is not shown if smaller than symbol. (sp=spring, sm=summer, au=autumn; first, second and third axes represented by -1, -2, and -3 respectively).

5.2.5 Conclusions

Regeneration of *Quercus ilex* occurred after each disturbance treatment. The common traits showed in this study were:

- High initial nutrient concentrations in leaves and stems allowing a high photosynthetic capacity (Field and Mooney 1986, Evans 1989).
- Differences between undisturbed and disturbed plots tended to decrease over time and no general differences to the 4th- and 5th axes were found.
- Lower N, P, S concentrations in summer.
- N and P mass variations on leaf area basis over time which showed the importance of resorption after disturbance. This supports the idea of a source-sink positive effect on resorption (Nambiar and Fife 1987, Chapin and Molainen 1991, Puignare and Chapin 1992).
- Higher N and P use efficiency compared to the undisturbed plot taking into account stem nutrient concentrations on the 1st- 2nd- and 3th axes and stem nutrient concentrations from the control plot with equivalent age.

Different traits were:

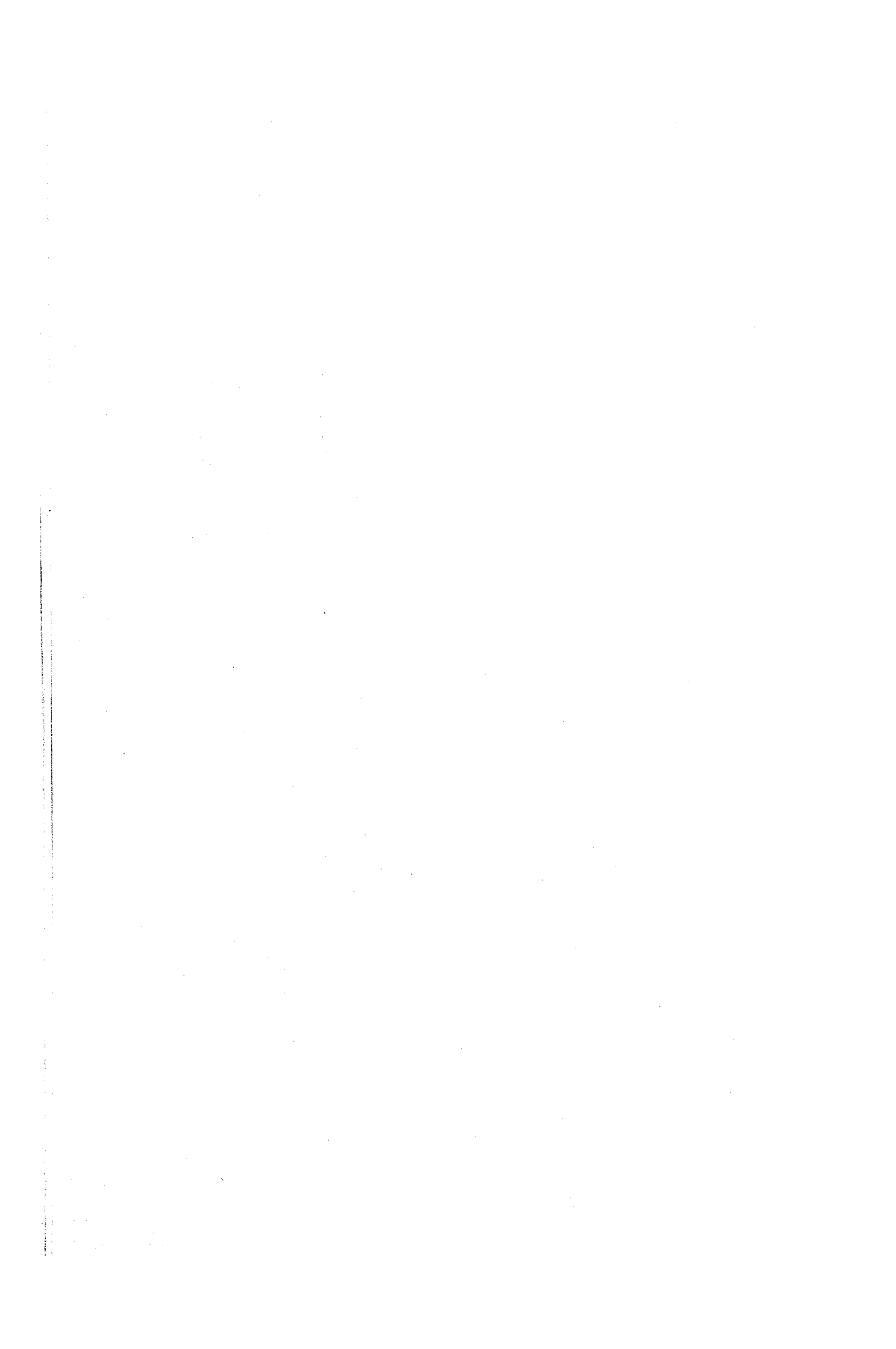
- Burned plot showed clear axes differentiation and lower N concentration values. Hence showing a higher N use efficiency than the other treatment plots.
- Clearcut plot showed lower initial nutrient mass on leaf area basis, hence lower retranslocation.
- Firebreak plot, according with a slower growth showed by a lower mean weight of Stems-1 (Sabaté and Gracia, unpublished manuscript, see chapter 5.1), showed a general lower K concentrations.

5.2.6. References

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6. CONCLUSIONS

Capítol 2

Les digestions àcides amb forn de microones domèstic per a la solubilització del P, K, Ca, Mg i S de mostres de teixits vegetals i la seva lectura analítica amb Plasma (ICP) són satisfactòries tant per la rapidesa de la digestió (permetent processar un elevat nombre de mostres) com per la seva fiabilitat. Aquestes dues característiques són imprescindibles davant de dissenys experimentals de camp que recullen un elevat nombre de variables d'interès en ecologia.

Capítol 3

La massa de nutrient per unitat de superfície de fulla és diferent entre el coster i la vall reflectint les diferències de disponibilitat entre la part alta o coster i baixa o vall (la darrera amb sòls més profunds) de la conca de l'Avic. A més, altres condicions ambientals com la pluja, la radiació anual i la temperatura són també importants perquè també determinen les característiques estructurals dels elements que componen la capçada. El pes específic de les fulles influeix la concentració de nutrients quan es refereix a pes sec de mostra, en diluir els nutrients de les fulles en matèria orgànica més estructural. Tant el pes específic, com l'índex foliar, com la biomassa total de fulles i la massa de nutrients que contenen les capçades estan relacionats amb les característiques ambientals esmentades.

A la vall s'ha trobat més massa de nitrogen i de magnesi per unitat de superfície de fulla. Això es pot associar a una més alta capacitat fotosintètica en aquest lloc, que estimula un bosc menys dens i més alt quan es compara amb el coster. A part que altres causes històriques de gestió forestal han pogut influir en aquestes diferències. En canvi, s'ha trobat més massa i concentració de potassi al coster que a la vall, fet que en principi pot estar relacionat amb un major control estomàtic al coster que a la vall (d'acord amb Anna Sala 1992).

El contingut de nutrients a les fulles al llarg del perfil vertical a la capçada així com la seva reabsorció decreixen des de la part alta a la part baixa de la capçada. Així, les fulles de la part inferior de la capçada tenen més restringit el magatzem de nutrients que poden ser reutilitzats.

Les variacions en la massa de nitrogen i fòsfor per unitat de superfície de fulla posen en evidència processos de descàrrega de nitrogen i fòsfor abans de l'estiu, i nova càrrega d'aquests nutrients en els períodes de menys producció que coincideixen amb temperatures més baixes i alta disponibilitat hídrica (de la tardor a principis de primavera). Aquestes masses de nitrogen i fòsfor poden alimentar part de les necessitats de nitrogen i fòsfor per a la construcció de noves estructures produïdes en períodes de creixement. Les variacions de massa de nitrogen i fòsfor a les fulles vives van ser més grans a la vall.

La reabsorció de nutrients de la fullaraca va ser lleugerament més alta pel nitrogen i més baixa pel fòsfor al coster. Així, la reabsorció més baixa de nitrogen a partir de fulles funcionals queda compensada per una reabsorció més alta a partir de la fullaraca. En canvi la reabsorció de fòsfor va ser sempre més alta a la vall. Probablement un major creixement a la vall estimula la reabsorció de nutrients per l'efecte conegut per *source-sink*.

L'eficiència en l'ús del nitrogen i el fòsfor en el compartiment aeri constituït per la capçada tendeix a ser més gran a la vall si ens fixem en la seva productivitat, més alta a la vall que al coster. Malgrat això, si ens fixem en l'invers de la concentració de nutrient com a índex d'eficiència les fulles al coster presenten valors més baixos, excepte pel potassi. Així que malgrat que és interessant obtenir l'eficiència en l'ús de nutrients en determinats compartiments de la planta com per exemple la capçada, també es necessita una visió global i una determinació de la distribució dels fotosintats a nivell de tota la planta.

Capítol 4

Diferències inter-annuals de les condicions ambientals en l'experiment de fertilització i d'irrigació han influenciat les característiques estructurals de la capçada a part dels canvis induïts per l'experiment, de manera que fulles i branquillons produïts en anys secs (1989) són més petits que els produïts en anys més humits (1988). Aquestes diferències ja es van observar abans del tractament (comparant 1987 amb 1988). Malgrat això, la producció de 1990 reflecteix més clarament els efectes de l'experiment donat que la irrigació es va poder començar a principis de primavera i no ja iniciat l'estiu (mitjans de juliol) com va succeir l'any 1989.

L'aigua i el nitrogen són els principals factors que limiten el creixement de l'alzina. Malgrat això l'efecte negatiu del fòsfor (aplicat en forma de superfosfat càlcic) no és clar. Els efectes negatius dels tractaments amb fòsfor possiblement es deuen a la interacció del calci amb el potassi en reduir l'absorció de potassi i per tant afectant el creixement de la capçada.

L'efecte de l'aigua queda clarament reflectit en les característiques estructurals dels elements que componen la capçada. Més pes i longitud dels brots així com de l'àrea de fulles. En canvi, contràriament al que esperaríem el pes específic de les fulles no és més baix en els tractaments amb aigua. Donat que la irrigació aplicada no ha modificat la radiació que arriba a les capçades, però en canvi la pluja sí que l'hagués modificat (degut als núvols), creiem que altres variables com la radiació incident semblen la causa més important que determina el pes específic.

L'efecte de l'aigua en la concentració de nutrients ha estat en general una

concentració més baixa en els tractaments amb aigua. Aquesta es pot explicar per una major producció en els tractaments amb aigua que ha donat com a resultat una dilució dels nutrients inclosos en una matèria orgànica més estructural.

L'efecte del nitrogen també ha quedat reflectit en un major creixement dels elements que componen la capçada. S'ha obtingut més pes mitja i longitud dels branquillons en aquest tractament. A més les fulles produïdes a la primavera de 1990 (menors d'un any) han presentat menys pes específic, i més pes i àrea mitjana. L'efecte del nitrogen en la concentració de nutrients ha quedat recollit en una major concentració a les fulles produïdes a la primavera de 1990 amb els tractaments de nitrogen.

L'aigua i el nitrogen han augmentat l'àrea nova de fulles i l'índex foliar, aquests efectes a la capçada s'han produït abans i de forma més accentuada en els tractaments amb nitrogen que en els tractaments amb aigua, però aquests últims a més han incrementat el diàmetre dels arbres (segons Mayor i Rodà). Per tant la distribució de la producció en la fertilització amb nitrogen sembla que s'ha dirigit més a les capçades que en el cas de la irrigació.

Els tractaments amb nitrogen han augmentat la reabsorció de nitrogen i fòsfor en les fulles produïdes a la primavera de 1987 abans de la seva caiguda. Això es pot relacionar amb la major producció de fulles noves i per tant amb l'augment de la demanda de nutrients (efecte *source-sink*). Els tractaments amb aigua han augmentat la massa de fòsfor reabsorbida però no el seu percentatge.

Els tractaments amb fòsfor han reduït l'àrea i pes mitjà de les fulles i la longitud mitjana dels branquillons. Això possiblement es pot explicar per la més baixa concentració de potassi en aquests elements i el seu paper en els processos d'expansió d'àrea foliar i de creixement en longitud dels branquillons. El tractament amb fòsfor no ha modificat la concentració d'aquest element.

Capítol 5

La regeneració de l'alzina ha estat un element comú en totes les pertorbacions practicades. Característiques comunes entre la parcel·la cremada, la parcel·la tallada arreu deixant les branques, i la parcel·la tallada arreu i neta (tallafocs) han estat fulles de mida més gran en els rebrots que a les alzines no pertorbades. Les diferències han estat a les fulles de l'eix de creixement principal. A mesura que han anat apareixent nous eixos de creixement les característiques estructurals de les fulles i branquillons dels rebrots s'han acostat més a les del bosc no pertorbat. Així, les diferències amb el bosc no pertorbat, han desaparegut a les fraccions produïdes durant el segon any després de la pertorbació. Fraccions distribuïdes bàsicament en els eixos de creixement d'ordre més gran (quart i cinquè eix de

creixement).

Els rebrots de la parcel·la tallada amb branques han presentat diferències estructurals a les etapes inicials del seu creixement degut a la intercepció de la llum produïda per les branques tallades i deixades. Això s'ha reflectit en un creixement inicial més gran en l'eix principal i un menor desenvolupament lateral de la capçada, així com també un menor pes específic. Aquestes diferències han desaparegut un cop s'han superat les branques deixades a la parcel·la. La parcel·la tallada i neta (tallafocs) ha presentat un menor creixement com reflecteixen una menor *àrea de fulla / àrea basal* i un menor pes mitjà de l'eix principal dels rebrots. De totes maneres, les diferències entre els tractaments han anat disminuint al llarg del temps durant el període d'estudi.

L'alta concentració de nutrients a les fulles i branques dels rebrots, poden permetre una alta capacitat fotosintètica (mesurada per Fleck et al. 1993) però també un magatzem de nutrients que poden alimentar la nova producció (molt activa en aquestes etapes inicials). Les concentracions de nitrogen, fòsfor i sofre tendeixen a ser més baixes als estius i més altes a la tardor i la primavera, períodes en què el creixement és més baix.

Les variacions temporals de la massa de nitrogen i fòsfor per unitat de superfície de fulla posen en evidència la importància de la reabsorció de nitrogen i fòsfor en aquestes etapes inicials de creixement que poden alimentar les noves estructures produïdes. Aquesta reabsorció es pot interpretar com un cert grau d'internalització dels nutrients en aquestes etapes inicials després de la pertorbació, en què poden ser exportats, per exemple, per erosió. De tota manera, s'hauria de determinar la importància quantitativa de les reserves de nutrients a les soques per poder relativitzar la proporció d'internalització que s'ha donat després de la pertorbació respecte de la que s'ha donat en acumular nutrients en forma de reserva durant els períodes en què l'alzinar no ha estat pertorbat.

En definitiva

Podem afirmar que l'alzina presenta una gran plasticitat pel que fa als elements que componen la seva capçada en relació a les disponibilitats d'aigua i nutrients. Aquesta plasticitat que queda recollida en mesures com el pes mitjà de les fulles i la seva àrea mitjana així com el pes mitjà i la longitud dels branquillons. El contingut de nutrients també recull les diferències de disponibilitat d'aquests elements. En general s'observen a les fulles d'alzina, valors més baixos de nitrogen i fòsfor als estius i valors més alts a la tardor i la primavera. Això corrobora l'existència de la reabsorció d'aquests elements al llarg de la vida de les fulles i per tant un cert paper d'aquests processos en el suministre de nutrients en els moments de creixement a la primavera.

7. APÈNDIX

Canopy Structure of a *Quercus ilex* forest: Site and seasonal variability in relation to water availability

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Key Words: *Quercus ilex*, canopy structure, leaf area index, water deficits, mediterranean sclerophylls.

Summary

Spatial and temporal changes in canopy structure were studied over a two year period in a mediterranean *Quercus ilex* forest in Catalonia (northeastern Spain). Destructive sampling during 1988 and 1989 was conducted in parallel at two locations within the watershed (referred to as ridge top, at 975 m and valley bottom, at 700 m) which represent the endpoints along gradients in elevation, aboveground microclimate, and water availability. Due to differences in soil water recharge during the previous fall, winter, and spring, water availability during the 1988 growing season was higher than that experienced by trees during the growing season of 1989. At both sites studied, similar inter-annual changes in canopy structure were observed in response to differences in water availability. For samples harvested in the upper 50 cm of the canopy, these changes included both a decrease in average leaf size and a decrease in the ratio of young (less than one year old) to old (one year or older) leaf and stem biomass during the drier year (1989). At the whole canopy level, a decrease in leaf production efficiency (ratio of new leaves and stems to old leaf biomass) and an increase in the stem to leaf biomass ratio was observed in 1989 as well. Temporal changes in total canopy leaf area index (LAI) were not statistically significant. Despite differences in stature and density of trees at the ridge top and valley bottom sites, average LAI values of *Quercus ilex* were not significantly different (4.6 m² m⁻² and 5.3 m² m⁻², respectively). Vertical distribution of leaves and stems within the canopy was very similar at the two sites. A uni-modal distribution of LAI was found with more than 60% of the total LAI in the uppermost meter of the canopy. The possible significance of such an LAI distribution on the canopy carbon budget is discussed.

Introduction

The structure of vegetation canopies, as determined by the spatial arrangement of its elements, is the integrated result of selection in response to a variety of environmental conditions and competitive interactions. The systematic variation in the physical and biological characteristics of foliage with canopy height documented in different forest and shrubland ecosystems. (Eckardt *et al.* 1978, Caldwell *et al.* 1986, Hutchinson *et al.* 1986, Hollinger 1989, Parker *et al.* 1989) suggests that canopy architecture is optimized for light interception and maximize carbon gain under the particular habitat conditions experienced by the plant.

Because cell growth is very sensitive to water deficits (Hsiao 1973), reductions in available water may be accompanied by reductions in leaf surface area. Studies on the spatial variability in total leaf area index (LAI) in forests have shown LAI to decrease as site water availability decreases (Grier and Running 1977, Waring *et al.* 1978, Gholz 1982, Gholz *et al.* 1990) and as the resistance to water flow through the canopy simultaneously increases (Specht and Specht 1989). In addition to the seasonal LAI variation encountered in forests (Vose and Swank 1990), year to year changes in water availability may also contribute to inter-annual LAI variation. Thus, LAI estimates based on destructive measurements carried out over short periods of time can be strongly biased.

Photosynthetic activity in mediterranean sclerophyll shrubs and trees occurs year-round if habitat conditions are favourable. However, carbon dioxide uptake is often decreased due to suboptimal temperatures during winter (from mid-December to mid-March) and to soil water deficits and high evaporative demands during summer (from mid-June to mid-September). Production of new leaves occurs mainly during the spring when soils are recharged with water and during this period maximum photosynthetic rates are observed (Tenhunen *et al.* 1987a). When accumulated rainfall during the previous fall and winter is low and soils are not completely recharged, water deficits may develop during late spring and become severe during the summer months. In addition to the reduction of leaf gas exchange via stomatal mechanisms observed in mediterranean sclerophylls (Tenhunen *et al.* 1987b, Rhizopoulou and Mitrakos 1990), whole plant reduction in exposed leaf area has been cited as a response to the intensity and duration of the drought period at different sites (Poole and Miller 1981, Rambal and Leterme 1987). However, in the short term intra- or inter-annual variations in LAI have seldom been documented, very little quantitative information exists about canopy structural changes of mediterranean sclerophylls in response to water availability.

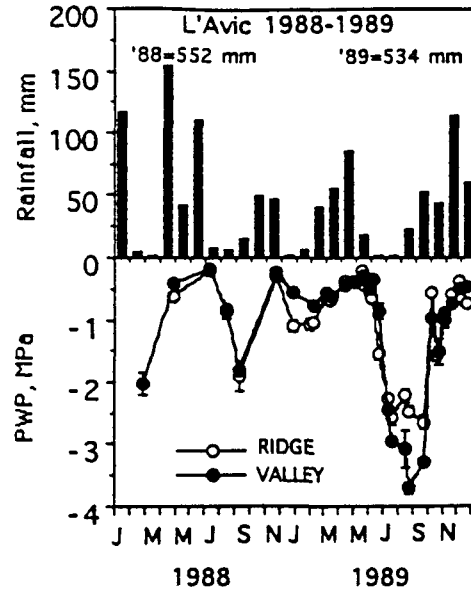


Figure 7.1. Upper panel: monthly precipitation measured at L'Avic watershed during 1988 and 1989. The annual totals are also indicated. Lower panel: Seasonal course of the pre-dawn xylem water potential (PWP) measured in terminal shoots of the upper crown of *Quercus ilex* trees at the Ridge Top and Valley Bottom sites. n ranges from 3 to 6. Vertical bars indicate standard error of the mean (from Sala 1992).

Table 7.1. Some characteristics of the two permanent sampling sites. G: Global shortwave radiation incident above the canopy; Ea: actual evapotranspiration; Eo potential evapotranspiration.

	RIDGE	VALLEY
Elevation (m)	975	700
Soil depth (cm) ^a	47	86
Tree height (m)	3-6	8-12
Tree density (stems ha ⁻¹) ^b		
<i>Quercus ilex</i>	9314	3491
<i>Quercus pyrenaica</i>	43	0
<i>Arbutus unedo</i>	0	3273
<i>Phillyrea media</i>	29	1527
<i>Vivurnum tinus</i>	0	473
G (GJ m ⁻² yr ⁻¹)	5.7	4.9
Ea Eo ⁻¹ ^a	<0.95	≈1
T (°C)	12.8	13.9

Data not obtained in this study are from (a) Piñol (1996) and (b) Lledó (1990).

The investigations described here are part of a more general study on the canopy water use and hydrological balance of a Mediterranean watershed (l'Avic, Catalonia, Sapin) dominated by *Quercus ilex*. The ultimate goal is to understand controls on seasonal and spatial patterns in canopy water use (Sala 1992), to understand the subsequent effect of these patterns on the hydrology of the entire watershed (Piñol *et al.* 1991), and to develop a predictive model of water use that will allow examination of catchment water balance with respect to a variety of scenarios related to longer-term climate change. Distinct environmental gradients exist at l'Avic, with greater soil depth for water storage and a reduced radiation load at valley bottom sites as compared to the upper slopes. Along this gradient, there are obvious changes in tree height, density and trunk diameter. A primary goal of the present study was to determine whether canopy LAI at the lowest valley bottom sites was greater than that on the upper slopes. We were also interested in determining whether long-term differences in site water availability might be responsible for site-specific variation over time in canopy structure. Our third objective was to obtain an average description of forest canopy structure at these two sites for modelling purposes.

Methods Study Area

L'Avic watershed (41° 15' N-1° E) is located in the Prades Mountains (Catalonia, NE Spain), 30 Km from the Mediterranean coast. The watershed occupies 51.6 ha, ranging from 680 to 1007 m in elevation. The average slope is 25.8° facing N-NW. *Quercus ilex* L. (holm oak) forms essentially pure stands throughout the study area. Soils in L'Avic develop directly on rocky substrata or on top of a colluvial layer. Soils are xerochrepts of variable depth, which tends to increase in the lower parts of the watershed (Piñol 1990). Climate is typically Mediterranean, with an annual mean temperature of 13.8° C and annual mean precipitation (mostly as rain) of 658 mm. The dry period extends from mid-June to mid-September (period 1957-1988). There is a substantial year to year variability in both the amount and in the seasonal distribution of precipitation. Figure 7.1 shows the distribution of precipitation during the study period (1988-1989) at l'Avic. Even though the annual totals are very similar, there were important differences in the seasonal distribution. The fall of 1988 and the winter and spring of 1989 were drier, as compared to the fall of 1987 (not shown) and the winter and spring of 1988. As a result, the summer of 1989 was considerably drier than the summer of 1988.

Sampling Sites

Two sampling sites were located in l'Avic watershed at the ends of a gradient in elevation, microclimate and forest structure: 1) at the bottom of the valley, at 700 m altitude, near to the stream, sheltered by the steep valley slopes (valley bottom site), and 2) on the upper open slopes, approximately 30 m below the ridge of the

mountain, at 975 m altitude (ridge top). The main differences of the forest at the two sampling sites are indicated in Table 7.1. Stands on upper slopes of the watershed have a much higher density of stems per ha than stands in the lower areas. *Quercus ilex* resprouts vigorously after coppicing, which was prevalent on the upper slopes along access roads until approximately 1950. Nevertheless, little disturbance has occurred since that time and structure is considered to have equilibrated with environmental differences between the two sites. Lledó (1990) provides a detailed analysis of the altitudinal heterogeneity in vegetation distribution. Microclimate differences between sampling sites result mainly from topographic differences. Global shortwave radiation incident above the canopy (Table 7.1) was estimated using the model of Gracia (1984). Estimates at the valley bottom site differed less than 2% with actual measurements conducted during 1989 (Sala 1992). Estimated annual global shortwave radiation is lower at the valley bottom than the ridge top (Table 7.1) due to the effect on the interception of solar radiation by the steep lateral mountain slopes. Wind velocity is significantly lower at the valley bottom than at the ridge top (Sala 1992) and average daily temperature measured simultaneously at both sites is lower at the ridge top (Table 7.1). Bellot and Escarré (1991) did not find significant differences in total precipitation between two sampling stations located at 720 m and 960 m within l'Avic watershed, but there are apparent differences in soil water availability between the ridge top and valley bottom sites. After simulating the spatial heterogeneity of the actual evapotranspiration (E_a) in l'Avic watershed with a hydrological model that incorporates the topographic variability of the terrain, Piñol (1990) found that only in the lowest parts of the valley near the stream did simulated E_a values equal the potential evapotranspiration (E_o). In the remaining area of the watershed the ratio (simulated E_a)/ E_o is below 0.95, indicating that soil water reserves are not always sufficient to supply atmospheric evaporative demand.

The average rate of foliage turnover in *Quercus ilex* at sites in Catalonia is about 2.4 years (Lledó 1990). Growth occurs mainly during the spring (May to June) and, to a lesser degree, if water stress and soil water deficit during the summer are not severe, in early autumn (October). Litterfall patterns during the year are related to periods of new leaf production, degree of water stress during summer and cold stress during winter. Periodic measurements of litterfall at l'Avic forest from 1982 to 1988 indicated that 84% of the mean total occurred between April and August (Bellot *et al.* 1992).

Biomass Harvests

Sampling of canopy elements were conducted in parallel at the ridge top and valley bottom sites during mid-summer of 1988 (late July and early August), late fall 1988 (late November and early December), early spring 1989 (early April, before the new growth period), mid-summer 1989 (August), and late fall 1989

(late November). Access to the canopy to sample foliage and branches was obtained using a 11 m tall aluminum ladder. The ladder was set up vertically to avoid canopy disturbance, and fixed with nylon ropes to the ground and to main trunks of neighbouring trees. During each sampling period, three randomly located square columns ($0.5 \times 0.5 \text{ m}^2$) were defined at the ridge top and valley bottom sampling sites using an extensible mast traversing from the ground to the top of the canopy. The columns were delineated with nylon strings stretched from a metallic frame (0.5 m on a side) mounted at the top of the mast, to one 10 cm above the forest floor. Only in very few cases was the main trunk of a tree included in the sample column. All branches less than 2 cm in diameter (with or without leaves) contained in the column were collected at 0.5 m intervals from the top to the bottom of the canopy and stored in labelled plastic bags. The length and diameter (measured at both extremes) of the branches larger than 2 cm in diameter were recorded in the field. Samples were transported to the laboratory and kept in a dark freezer (-1°C) until samples were analyzed. Young (less than 1 year) and old (1 year or older) leaves and branches in each sample were separated. Senescent leaves (brown or with obvious symptoms of senescence) were also separated. Subsamples of leaves and branches for each category were taken to calculate the ratio of dry weight to projected area. The projected area of leaves and branches was measured, respectively, with a leaf area meter Li-3000 (LiCor Inc.) and an IBAS image analyzer. Projected area of branches was only measured from samples collected in 1989. Because of the nature of the leaves (hard and often rolled or wavy), leaf subsamples were pressed and moistened with warm steam before determining leaf areas. Leaf and branch subsamples and the remaining sample for each category and canopy level were oven dried at 65°C for 72 h. The ratio dry weight to area obtained for each subsample was applied to the total dry weight of the corresponding category to calculate the total projected area for each canopy layer. Projected area calculated from the field measurements of branches larger than 2 cm in diameter was added to the fraction of branches 1 year or older to obtain the corresponding projected stem area. Average surface area (cm^2) of young, old, and senescent leaves in the different canopy levels was obtained from the area and number of leaves of the corresponding subsample. Similarly, specific weight of young, old, and senescent leaves was obtained from the total dry weight and area of the corresponding subsample.

Variables analyzed in this study are: total canopy leaf and stem area index (LAI and SAI, respectively, measured as total projected leaf or stem area on a ground area basis, m^2m^{-2}), leaf surface area (cm^2), leaf specific weight (LSW, g cm^{-2}), ratio of stem to leaf biomass (g g^{-1}), ratio of young to old leaf biomass (g g^{-1}), ratio of young to old stem biomass (g g^{-1}), and leaf production efficiency (ratio of grams of new twigs and leaves vs. grams of existing leaves, g g^{-1}). The canopy vertical distribution of LAI, SAI, leaf size and LSW was also analyzed. Because of the low number of samples in which the main trunks were included, calculations of stem area index (SAI) and of stem biomass do not include the main

Table 7.2. Total canopy leaf area index of *Quercus ilex* (LAI, m^2m^{-2}) and leaf area of senescent leaves (Sen. m^2m^{-2}) measured during 1988 and 1989 at the ridge top and valley bottom sites of L'Avic watershed. Data are the mean of 3 columns 0.5 x 0.5 m a side. In parenthesis are standard errors.

SITE		summer 88	fall 88	spring 89	summer 89	fall 89
Ridge	LAI	4.66±0.23	3.58±0.50	5.62±1.41	3.86±0.93	5.23±1.26
	Sen.	0.007±0.007	0.006±0.005	0.006±0.004	0.006±0.003	0.011±0.007
Valley	LAI	5.04±1.01	4.98±1.34	5.08±0.15	5.86±0.15	5.44±0.53
	Sen.	0.002±0.002	0.004±0.004	0.024±0.007	0.180±0.058	0.010±0.008

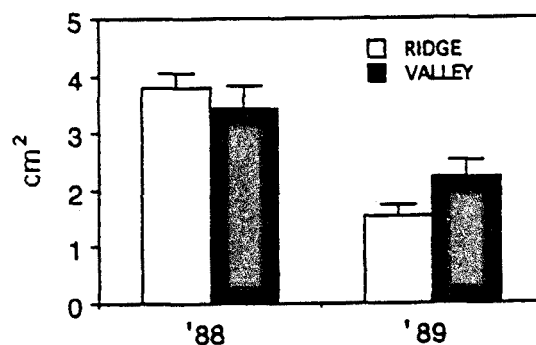


Figure 7.2. Average leaf surface area of leaves less than one year old harvested in the upper 0.5 m of the canopy during 1988 (n=9) and 1989 (n=6). Vertical bars indicate standard error of the mean.

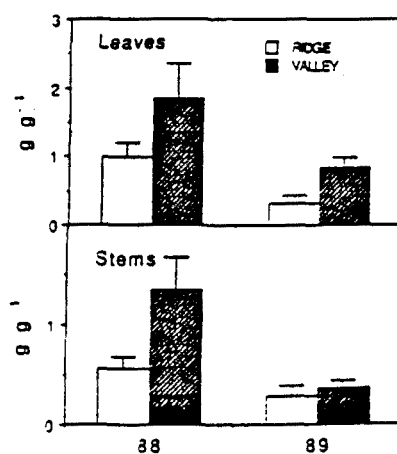


Figure 7.3. Ratio of young to old leaf (upper panel) and stem (lower panel) biomass in samples harvested in the upper 0.5 m of the canopy during 1988 (n=9) and 1989 (n=6). Vertical bars indicate standard error of the mean.

trunks. Site and seasonal differences in the variables considered (see below) were tested with a two-way analysis of variance using the PROC GLM (general linear models) of the Statistical Analysis System (SAS Institute, 1988). The value of the arcsine of the square root of ratios such stem of leaf biomass, young to old leaf and stem biomass, and leaf production efficiency was used to normalize the data. To emphasize the effects of water availability on canopy structure, analysis on site and temporal differences in LSW, leaf size, ratio of young to old leaf biomass, and ratio of young to old stem biomass was restricted to the upper 50 cm of the canopy, where light is not a limiting factor for carbon assimilation and subsequent growth.

Results

Temporal trends

Total canopy leaf area index (LAI) values for *Q.ilex* at the ridge top and valley bottom sites at different times during 1988 and 1989 are shown in Table 7.2. Although seasonal differences were not statistically significant, there were clear site-specific structural changes in response to differences in water availability during 1988 and 1989 at the two sampling sites. For instance, a significant increase of the area of senescent leaves was observed at the valley bottom site at the end of the summer of 1989 (Table 7.2). This is because trees at the valley bottom experienced greater water stress during the summer of 1989 than did trees at the ridge top (Sala 1992). This is reflected by the substantially lower pre-dawn water potential in *Q.ilex* measured during this period (Figure 7.1), in the valley bottom.

To compare growing seasons, samples from summer '88, fall '88, and spring '89 (before the new growth of 1989 occurred) were pooled to represent leaves and twigs produced during 1988, and samples from summer '89 and fall '89 were pooled to represent those produced in 1989. Leaves from the upper 50 cm of the canopy during 1989 at both sampling sites were smaller than the ones sampled in 1988 (Figure 7.2, $p < 0.0001$). Similarly, the ratio of young to old leaf biomass and of young to old stem biomass in the upper 50 cm of the canopy decreased in 1989 (Figure 7.3, $p < 0.02$). Leaf production efficiency in the upper 50 cm of the canopy (ratio of leaves and stems to old leaf biomass) also decreased in 1989 but differences were only significant at the ridge top ($p < 0.05$, not shown). At the whole canopy level, the ratio of total canopy stem to leaf biomass on a ground area basis increased (Figure 7.4a) and the leaf production efficiency decreased in 1989 ($p < 0.006$; Figure 7.4b). Despite these changes, mean canopy LAI of *Q. ilex* in 1988 was not significantly different from 1989 at either of the two sampling sites.

New leaves produced in the upper 50 cm of the canopy had higher specific weight

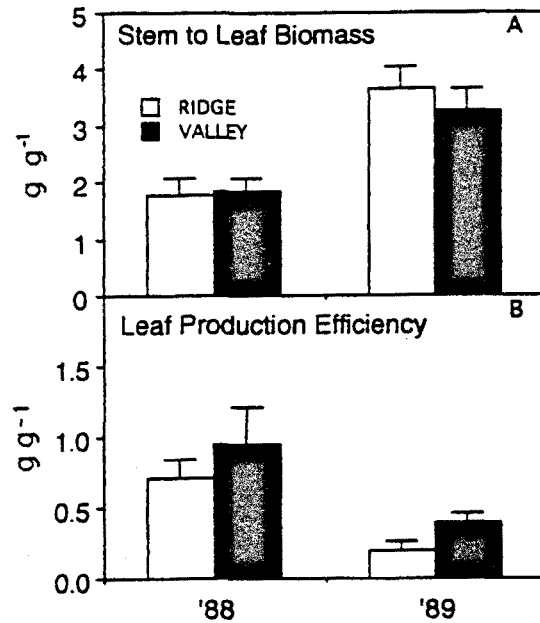


Figure 7.4. Ratio of (A) stem (excluding main trunks) to leaf biomass, and (B) leaf efficiency production (i.e. grams of new leaves and twigs produced per gram of existing leaves) for the entire canopy in samples harvested during 1988 (n=9) and 1989 (n=6) at the ridge top and valley bottom sites. Vertical bars indicate standard error of the mean.

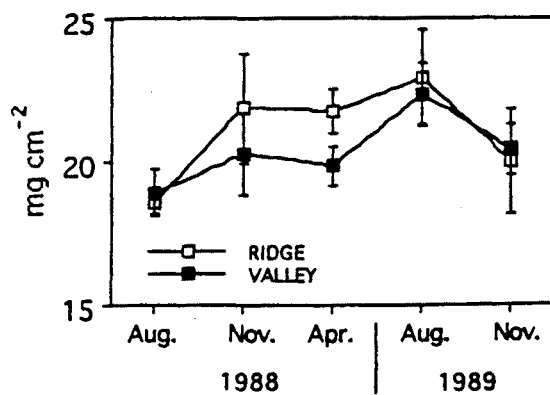


Figure 7.5. Changes in leaf specific weight of leaves harvested in the upper 50 cm of the canopy at the ridge top and valley bottom sites. Samples were harvested beginning two months after initial growth in 1988 and for a period extending through the fall of 1989. Vertical bars indicate standard error of the mean (n=3).

Table 7.3. Leaf area index of *Quercus ilex* (m²m⁻²) and understory species averaged from 15 columns 0.5 x 0.5 m on a side harvested at the ridge top and valley bottom sites in L'Avic watershed. In parenthesis are standard errors.

SPECIES	Ridge	Valley
<i>Quercus ilex</i>	4.6 (0.42)	5.3 (0.31)
<i>Hereda helix</i>	0	0.360
<i>Arbutus unedo</i>	0	0.110
<i>Phillyrea media</i>	0	0.077
<i>Virburnum tinus</i>	0	0.068
<i>Sorbus aria</i>	0	0.054
<i>Lonicera implexa</i>	0	0.006
Other species	0	0.035
Total understory	0	0.7 (0.33)
Total	4.6 (0.42)	6.0 (0.31)

(LSW) in summer 1989 than in 1988 at both sites (not shown) but differences were not statistically significant. Changes in LSW of leaves sampled in the upper 50 cm of the canopy beginning two months after initial growth and for a period of more than one year is shown in Figure 7.5. At both sites, LSW increased until summer of 1989 (when leaves reached one year of age) and thereafter decreased. The observed seasonal trends were very similar at the ridge top and valley bottom sites, but seasonal changes in LSW were not statistically significant.

Site differences

Total canopy LAI (including understory species) obtained from the pooled mean of all samples (at total of 15 columns per site) was 4.6 +/- 0.4 s.e. m² m⁻² at the ridge top and 6.0 +/- 0.3 s.e. m² m⁻² at the valley bottom (Table 7.3). No understory species were present at the ridge top, but at the valley bottom site *Hereda helix*, *Arbutus unedo*, *Phillyrea media*, *Virburnum tinus* and *Sorbus aria* (in order of importance) were common understory species. LAI of the understory in the valley bottom was 0.7 +/- 0.3 s.e. m² m⁻². The corresponding LAI for *Q. ilex* was 5.3 +/- 0.3 s.e. m² m⁻². Because of the presence of understory at the valley bottom, site differences in total canopy LAI (including understory) were significant (p<0.02), but LAI of *Q. ilex* at both sites was not significantly different.

Projected stem area index (SAI, excluding main trunks) of *Q. ilex* obtained from the pooled mean of samples harvested in 1989 was very similar at both sites (1.34 +/- 0.38 s.e. $\text{m}^2 \text{m}^{-2}$ at the ridge top and 1.25 +/- 0.21 s.e. $\text{m}^2 \text{m}^{-2}$ at the valley bottom). SAI of the understory at the valley bottom was 0.11 +/- 0.07 s.e. $\text{m}^2 \text{m}^{-2}$. The ratio of young to old leaf biomass and young to old stem biomass (Figure 7.3) in the upper 50 cm of the canopy were both greater ($p < 0.05$) at the valley bottom than at the ridge top. There were no site differences leaf production efficiency, nor in the ratio of stem to leaf biomass (Figure 7.4). The latter, however, did not include main trunks. Leaf specific weight (LSW) and leaf size were also very similar at both sites, even though LSW tended to be higher at the ridge top (Figure 7.5).

Vertical organization

Canopies were 8-12 m high at the valley bottom and 3-6 m at the ridge top (Table 7.1). The vertical distribution of LAI at both sites (Figure 7.6) was uni-modal, with more than a 81% of the total LAI accumulated in the upper 2 meters of the canopy (60% in the uppermost m). The leaf area distribution profile was very similar at both sites. The ratio of projected area of young (less than 1 year) to old leaves (one year or older) in layers of equal depth decreased from the top to the bottom of the canopy.

Figure 7.7 shows the vertical distribution of the projected stem area index (SAI, excluding main trunks). At both sites SAI is slightly greater in the upper part of the canopy. Stems contribute 19% and 23% to the total phytomass projected area (leaves and stems) at the valley bottom and ridge top, respectively. Due to differences in tree density and stature, branches and leaves at the ridge top were distributed throughout the canopy, almost reaching to the forest floor, while at the valley bottom, the lowest leaves and stems were found 2 to 5 m above the forest floor.

Both LSW and leaf surface area of mature leaves varied with depth in the canopy. LSW was highest in the top layers of the canopy and decreased with depth (Figure 7.8a). Leaf surface area increased from the top to the bottom of the canopy (Figure 7.8b). This increase was greater at the valley bottom site than at the ridge top.

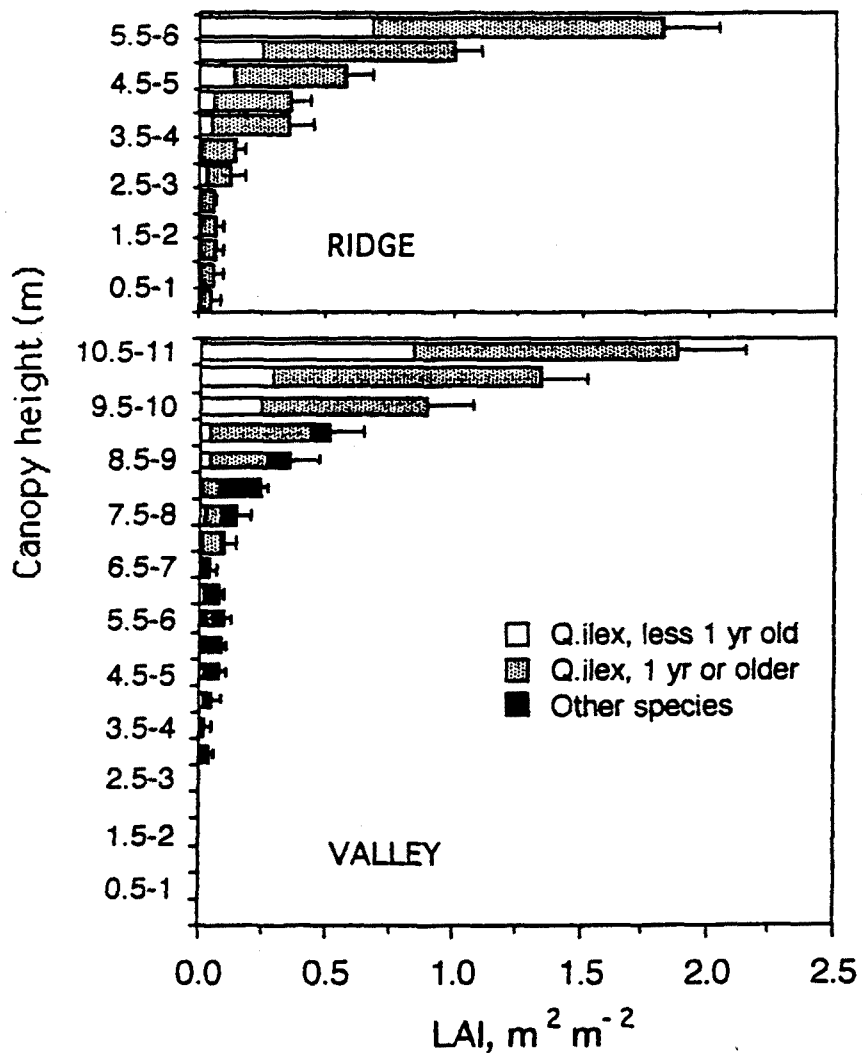


Figure 7.6. Canopy vertical distribution of the leaf area index ($\text{m}^2 \text{m}^{-2}$) at the ridge top and valley bottom sites. Data were averaged from a total of 15 vertical profiles (columns $0.5 \times 0.5 \text{ m}$ on a side) per site. Horizontal bars indicate standard error of the mean.

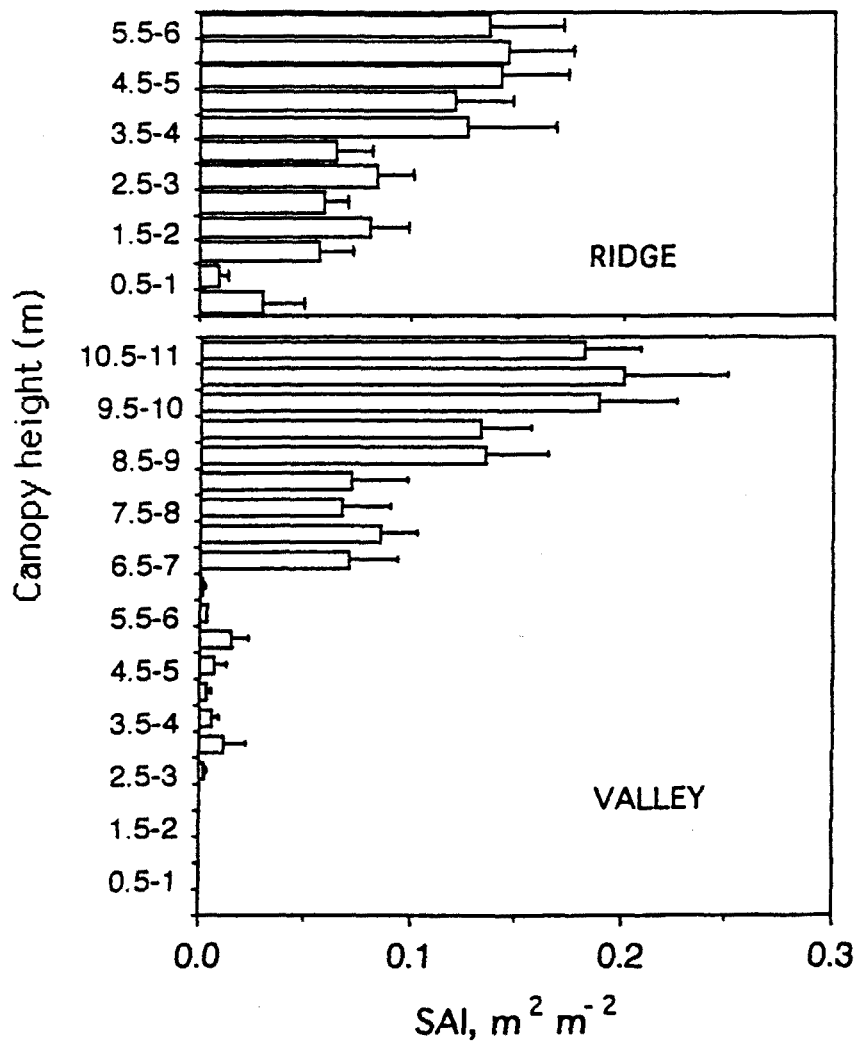


Figure 7.7. Canopy vertical distribution of the projected stem area index ($\text{m}^2 \text{m}^{-2}$, excluding main trunks) at the ridge top and valley bottom sites. Data were averaged from a total of 15 vertical profiles (columns $0.5 \times 0.5 \text{ m}$ on a site) per site. Horizontal bars indicate standard error of the mean.

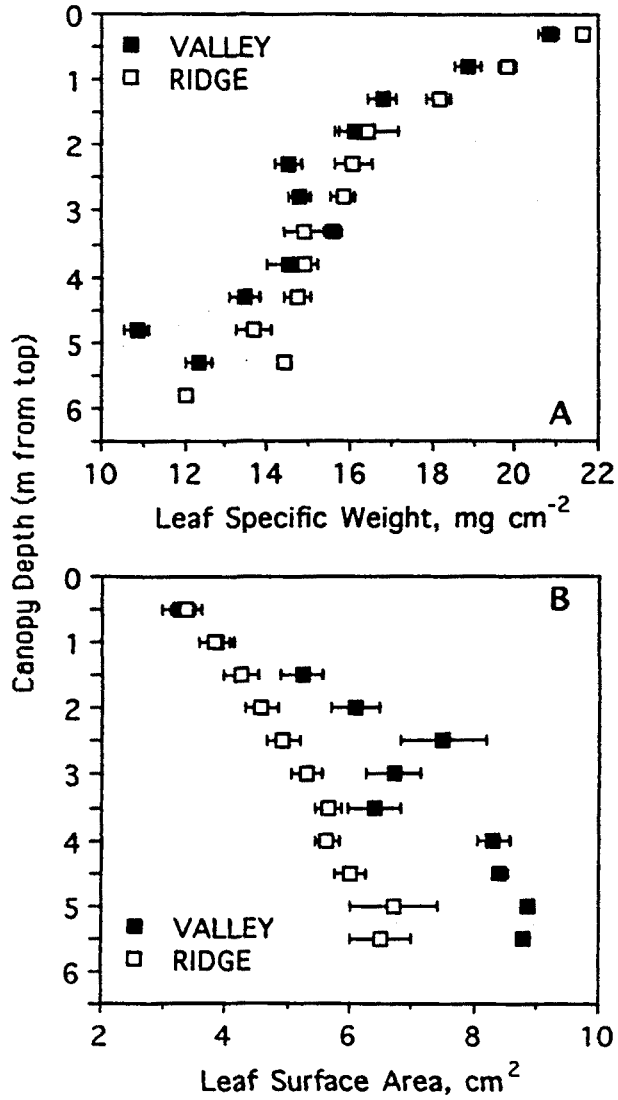


Figure 7.8. Vertical variation of the leaf specific weight (A) and average leaf surface area (B) of mature leaves. Data were averaged from a total of 15 vertical profiles (columns 0.5 x 0.5 m on a site) per site. Horizontal bars indicate standard error of the mean.

Discussion

Temporal trends

Inter-annual changes in canopy LAI of *Quercus ilex* in response to differences in water availability are suggested from the trends observed during 1988 (wet year) and 1989 (dry year), although it was not possible with our sampling scheme to establish their statistical significance. Responses, such as an increase in leaf abscission (cf. Table 7.2) and reduction of leaf extension (Fig. 7.2), are well documented for other species under water limiting conditions (Woodward 1987) and probably contribute to decreases in LAI at l'Avic. A statistically significant increase in senescent leaves remaining on branches was only established during the summer of 1989 for the valley bottom site. Periodic visual observations (every two weeks) during the entire study period confirmed that rapid leaf shedding did not occur between the observations reported here, and that a substantial increase of leaf senescence and mortality only occurred at the valley bottom site. Measured Xylem pre-dawn water potentials at this site during the summer of 1989 were substantially lower than at the ridge top, indicating greater seasonal water stress. Site differences in water stress during late summer appear to result from differences in soil water use during spring and early summer (Sala *et al.*, in prep.). Similar results were reported by Poole and Miller (1981) who found that pre-dawn water potential of chaparral sclerophylls on N-facing slopes were lower than those measured in S-facing slopes. Drying of the soil profile is related to stomatal controls, to total conductance for water through the soil-plant-atmosphere system, and to watershed hydrological processes which determine soil water storage at the beginning of summer drought. The effect to these factors on site water relations are examined further in a separate report (Sala *et al.*, in prep.). Even though a significant increase of senescent leaves was found only at the valley bottom site, LSW tended to be higher (although not significantly) at the ridge top than at the valley bottom (Fig. 7.5). LSW showed a tendency (although not statistically significant) to decrease at both sites after the dry season in 1989. This could be indicative of nutrient and stored assimilates being used or retranslocated to other parts of the plant.

The observed decrease in the ratios of young to old leaf and stem biomass in the upper 50 cm of the canopy (Fig. 7.3), and of the leaf production efficiency for the whole canopy (Fig. 7.4) in 1989 as compared to 1988, reflects reduced growth in response to water shortage. Rambal and Leterme (1987) reported a decrease in aboveground production of the mediterranean shrub *Quercus coccifera* along a water availability gradient from mesic to xeric sites, but there is little data on inter-annual changes in production in mediterranean sclerophylls at single sites. The increase in the ratio of canopy stem to leaf biomass in 1989 (Fig. 7.4) also indicates a reduction of leaf production in response to reduced water availability. Thus, the relative rates of turnover of stem and leaf materials seem to be more

responsive to environmental constraints than is canopy LAI. As suggested by Schulze (1986), a depletion of water modifies the carbon partitioning to favour growth of supporting organs and thus to improve the uptake and transport of available resources. Canadell and Rodà (1991) were able to document an increase in the root: shoot ratio of *Q. ilex* trees growing in a xeric site as compared to trees from a mesic site.

Site differences

Understory species were only present at the valley bottom site (Table 7.3). Because of the understory, total canopy LAI (all species) was higher at the valley bottom than at the ridge top. Forest stands found in the valley bottom are related to the typical lowland *Q. ilex* formation (*Quercetum illicis galloprovinciale*, sensu Braun Blanquet), while forest at the ridge top is the montane variant characteristic of higher altitudes (*Quercetum mediterraneum montanum*). Folch and Velasco (1978) describe both associations in the Prades Mountains and recognize a gradual altitudinal transition between the two communities.

The presence of understory species at the valley bottom site may be very important in terms of dry-down of the soil profile during summer as already discussed above. Greater LAI values (ca. $6.7 \text{ m}^2 \text{ m}^{-2}$ Hollinger 1989) have been reported for other montane evergreen forests than found for *Q. ilex* in our study at l'Avic ($4.6\text{-}5.3 \text{ m}^2 \text{ m}^{-2}$). On the other hand, Eckardt *et al.* (1978) and Gratani and Fiorentino (1988) also reported values for *Q. ilex* of approximately $4.5 \text{ m}^2 \text{ m}^{-2}$. These results suggest that this approximate LAI value may be near optimal for *Q. ilex*. Caldwell *et al.* (1986) suggested an optimal LAI of $5 \text{ m}^2 \text{ m}^{-2}$ in the related evergreen shrub *Quercus coccifera*. They found that in canopies with LAI greater than $5 \text{ m}^2 \text{ m}^{-2}$, very little light penetrated to lower canopy layers. PAR values below *Q. ilex* canopies range from 2% to 18% of the incident PAR above the canopy (Eckardt *et al.* 1978, Larcher and Tisi 1990), depending on time of the year and weather conditions. Ultimately, optimal LAI depends on the amount and arrangement of canopy elements, environmental conditions and available resources such as light, water and nutrients (Gholz 1982, Jarvis and Leverenz 1983, Gholz *et al.* 1990). These, in turn, affect photosynthetic efficiency, respiration costs, and carbon allocation to different sinks. *Q. ilex*, as many other mediterranean sclerophylls, exhibits a strong reduction of leaf gas exchange via stomatal mechanisms during either transient or extended periods of water deficit (Eckardt *et al.* 1978, Rhizopoulou and Mitrakos 1990, Sala 1992, Terradas and Save 1992). Tenhunen *et al.* (1990) examined the degree to which modification of physiological behavior vs. structural change influence the carbon and water balance for *Quercus coccifera* under typical mediterranean-type climate conditions. They suggested that physiological adjustments lead to larger reductions of water use than occur when leaf area is reduced from 3.5 to $1.5 \text{ m}^2 \text{ m}^{-2}$. The results of the present study support the idea that physiological and/or anatomical adjustments (for instance, in

xylem structure) are mechanisms that in sclerophyllous species like *Q.ilex* might be more effective for coping with limitations associated with the recurrent drought typical of mediterranean-type climates.

Vertical organization

Despite large differences in tree height, canopy vertical organization was remarkably similar at the ridge top and valley bottom sampling sites (Figures 7.6 and 7.7). There was a uni-modal leaf area distribution with 60% of total LAI accumulated within the uppermost meter of the canopy. Understory species at the valley bottom contributed 11% to the total canopy LAI without providing a second peak in LAI at lower canopy levels. Stems contribute 19 and 23% to the total phytomass projected area at the valley bottom and ridge top, respectively. This is a significant fraction that must be considered when using models of radiation extinction to estimate canopy gas exchange. The degree of change in LSW and leaf size with depth in the canopy was similar (Fig. 7.8) at both sites. In agreement with our results, Eckardt *et al.* (1978) and Gracia (1984) found a uni-modal distribution of LAI in *Q.ilex* 12 m in height. The decrease in leaf size at the top of the canopy is advantageous in terms of thermoregulation and heat dissipation (Gates 1980), especially since periods of greatest evaporative demand coincide with periods of high temperature and reduced water availability. During periods of heat stress, small differences in leaf temperature may have a great effect on reducing tissue mortality. The decrease in proportion of young leaves with respect to old from top to bottom of the canopy indicates a higher leaf turnover in upper parts of the canopy. Since leaf longevity tends to increase when carbon assimilation and growth are limited, the decrease in turnover rate of leaves from top to bottom of the canopy is probably a direct consequence of reduced light with depth in the canopy.

In contrast to the present study, Hollinger (1989) reported a bi-modal LAI distribution in an evergreen forest located in New Zealand. Hutchinson *et al.* (1986) and Parker *et al.* (1990) also reported bi-modal or even tri-modal LAI distributions in deciduous forests. A question of interest is why LAI is so strongly skewed to the upper parts of the canopy (the first meter in canopies from 5 to 12 m high) in mediterranean climates where leaves are more tightly coupled to the atmosphere. According to Horn (1971), mono-layer canopies are adapted to shady environments and are more effective during late successional stages while multi-layer canopies are more productive under open conditions and tend to appear in early successional stages. In *Q. ilex*, the tendency to accumulate most of the LAI in the upper canopy, is perhaps related to major activity in carbon uptake occurring during low light. During summer, midday stomatal closure limits carbon uptake to periods early and late in the day. The apparent high investment of mediterranean sclerophylls in leaf RuBP generation capacity also suggests tuning of gas exchange for optimal carbon uptake under low light conditions (cf.

Tenhunen *et al.* 1987b, their Fig. 10). Light harvesting per unit of leaf area remains high during spring, fall, and favorable winter weather conditions, when solar angle is still low and the risk of desiccation, either by low soil water or high evaporative demands, is reduced. In l'Avic, in particular, such a selective pressure would be reinforced by the topographic situation in a steep valley (mean slope of 25) facing N-NE. Larger and Tisi (1990) found that estimated daily carbon uptake in small shrubs of *Q. ilex* during fair winter conditions was substantially higher than carbon losses by respiration.

The analysis of the canopy structure in forests requires extensive sampling due to spatial heterogeneity. This is particularly true for *Q. ilex* forests (Floret *et al.* 1989). Indirect estimates of LAI such as obtained by examining the interception of direct-beam radiation within canopies (Vose and Swank 1990; Gower and Norman 1991) are useful in restricted situations for evaluating seasonal changes of LAI. However, their standard application in forest canopies is still limited due to the difficulty in differentiating between the amount of light intercepted by leaves, by trunks, and by branches, and the fact that leaves are often clumped, resulting in a highly anisotropic media within the canopy. Thus, we remain dependent on destructive methods such as the one used in this study which are extremely time consuming. More than 12 person-months of work were dedicated to collect and process the samples of this study. Increase in the sample size is in most situations impractical. Thus, our knowledge of structural changes in Mediterranean plant canopies over time continues to be restricted. Nevertheless, important site comparisons were made and the utility of several new variables as descriptors of change have been tested. The basic information obtained in this study provides data required for process models and allows us as well to formulate new hypotheses with respect to links between structure and function in Mediterranean forest ecosystems.

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