

## Influence of fire and tree-fell on physiological parameters in *Quercus ilex* resprouts

I Fleck, D Grau, M Sanjose, D Vidal

*Departament de Biologia Vegetal, Unitat de Fisiologia Vegetal, Facultat de Biologia, Universitat de Barcelona, Diagonal 645, 08028 Barcelona, Spain*

(Received 14 November 1994; accepted 8 January 1996)

**Summary** — Variations in the physiology of two kinds of resprout (originated after fire and after tree-fell) of *Quercus ilex* were analyzed under field conditions and compared with respect to the original, undisturbed vegetation, located within a Mediterranean watershed (northeast Spain). Resprouting vegetation of *Quercus ilex* after fire or after tree-fell showed, during the next growing seasons, enhanced photosynthesis, leaf conductance and Rubisco activity with respect to the original vegetation, especially under high temperature, irradiance and vapor pressure deficit (VPD). The lack of differences in nutrient (N, C, P, K and Ca) and soluble carbohydrate concentrations in leaves of resprouts originated after fire or after tree-fell indicates the independence of nutrients released by the action of fire and the contribution of underground organs. Differences in leaf mass per area (LMA) were due to increased thickness in resprouts whereas density was the same. N investment in chlorophylls or Rubisco was not different in control or either kind of resprout. The increased amount of carotenoids in resprouts contributed to providing protection from photoinhibitory processes.

***Quercus ilex* / fire / tree-fell / gas exchange / nutrients / photosynthetic pigments**

**Résumé** — Influence du feu et de l'élagage des arbres sur les paramètres physiologiques des rejets de *Quercus ilex*. On a étudié les caractéristiques physiologiques d'une végétation de *Quercus ilex* localisée dans une vallée méditerranéenne (nord-est de l'Espagne) après un incendie et l'élagage des arbres. Les résultats ont ainsi été comparés avec ceux d'une végétation sans aucune altération (expérience de contrôle). On a constaté que les rejets après un incendie et un élagage montrent, pendant les saisons de croissance suivantes, que la photosynthèse, la conductance des feuilles et l'activité Rubisco étaient supérieures par rapport aux feuilles de l'expérience de contrôle, et cela spécialement à hautes températures, irradiances et DPV. Le manque de différences en contenu minéral (N, C, P, K, Ca) et en carbohydrates solubles entre les feuilles des rejets après un incendie et après un élagage indique l'indépendance d'éléments nutritifs libérés par l'action du feu et la contribution des organes souterrains. Les différences de LMA (relation entre la masse des feuilles et la superficie de leur provenance) ont été le résultat du développement de l'épaisseur des rejets, tandis que la densité a été la même que celle des feuilles de contrôle. La quantité de N utilisée dans la chlorophylle ou

*la Rubisco n'a été différente dans aucune des situations. On a considéré l'augmentation des caroténoïdes dans le rejetons comme une protection face à la photo-inhibition.*

**Quercus ilex / feu / élagage des arbres / échange de gaz / contenu minéral / pigments photosynthétiques**

## INTRODUCTION

Rapid growth of resprouting vegetation has been observed in Mediterranean shrub ecosystems after fire (Christensen and Muller, 1975; Schlesinger and Gill, 1980; Saruwatari and Davis, 1989; Fleck et al, 1990, 1992, 1995) and after tree-fell (Castell, 1992; Sabaté, 1993). An extensive pre-existing root system of resprouting vegetation together with reduced shoot mass results in greater water availability to the growing resprouts (Radosevich and Conard, 1980; De Souza et al, 1986). Resprouts emerging in burned and felled sites have considerably more solar radiation available to them, due to the removal of the shading effect (Hulbert, 1988), which increases the photosynthetic capacity of resprouts (Knapp, 1984). Enhancement of photosynthesis and leaf conductance after fire has also been reported in chaparral species by Oechel and Hastings (1983), Hastings et al (1989), Thomas and Davis (1989) and Saruwatari and Davis (1989), but there is less information on European Mediterranean ecosystems (Trabaud and Méthy, 1988).

Higher N and P contents and leaf mass-to-area ratio (LMA) have also been described in postfire resprouts (Knapp, 1985; Reich et al, 1990). LMA tends to change in response to variations in nutrient availability (Gulmon and Chu, 1981) or in light intensity during growth (Björkman, 1981). Variations in leaf N content have been widely identified as a determinant of net photosynthetic capacity (Field and Mooney, 1986; Evans and Seemann, 1989); it depends on species, relative availabilities of N, P and other mineral nutrients, and

intrinsic ecophysiological characteristics (Reich et al, 1994).

In the present study, we compared leaf physiology of the resprouting vegetation of *Quercus ilex* after fire or tree-fell with that of the original stand, which had been undisturbed for 40 years. Soil nutrients in the felled stand were expected to be similar to control, whereas the burned stand should have exhibited a higher content originated from ash and char of above-ground material and litter.

We were interested in evaluating not only the effects of both kinds of perturbation, but also photosynthetic gas exchange in relation to water, nutrient and light availability, especially under environmental conditions that favor the midday depression of photosynthesis (Tenhunen et al, 1987; Correia et al, 1990).

## MATERIALS AND METHODS

### *Study site and experimental design*

The study was carried out in a holm-oak (*Quercus ilex*) forest at the Prades Experimental Complex of Catchments (Tarragona, northeast Spain) overlooking the Mediterranean Sea. The experimental plots are located on a steep slope (28°) at an elevation of 920 m and oriented south-southeast (41°21'N, 1°01'E). The main rock type in the area is schist and the soils are Lithic and Typic Xerochrepts (USDA Soil Taxonomy, 1975) (Serasolsas et al, 1992).

The site is a holm-oak forest that was managed until the 1950s as a source of charcoal, resulting in a multistemmed structure in the above biomass (now about 40 years old) and an older root system.

In August 1988, two 40 m x 20 m contiguous areas were tree-felled and trunks and large branches were uniformly distributed over the soil surface. In October 1988, one of these stands was burned; the fire front power was 9 350 cal cm<sup>-2</sup> s<sup>-1</sup>, which can be considered a medium value.

To compare the resprout physiological characteristics with the undisturbed *Q. ilex* trees, a control stand (40 m x 20 m) was available in a contiguous area.

The climate is typically Mediterranean, with cold winters, cool and wet springs and autumns and hot dry summers. The mean temperature is 13–14 °C and the annual precipitation, 500–700 mm.

### Plant material

At least six different root crowns (individuals) in the three different areas were randomly selected on each sampling day. *Q. ilex* leaves of lower canopy from the different crowns of undisturbed stand (control) were compared with resprouting leaves of crowns of burned and tree-felled stands, respectively. We selected only fully expanded leaves of the first flush after disturbances during all of the study period.

### Sampling

Experimental disturbances were not replicated in different areas due to problems related to the risk of fire spreading and conservation of protected areas. Before perturbances, the three areas had the same history, microenvironment

and soil characteristics (Serrasolsas, 1994) and were large enough to include different responses of the individuals (Sabaté, 1993).

Sampling was carried out five times in 1990 (15 months after fire and tree-felling) in winter, spring, early summer, late summer and autumn at the same time as the gas exchange measurements. Packets of ten leaves from different crowns of each stand were rapidly frozen in liquid nitrogen between 1200 and 1400 hours (local time) for Rubisco activity and photosynthetic pigment determination; they were later kept in the laboratory at –80 °C until assay. Moreover, 25–35 leaves from different crowns of burned, felled and undisturbed stands were collected for fresh weight (FW), dry weight (DW), mineral content and leaf area (LA) determinations. Environmental conditions (incident radiation [PAR], air and leaf temperature, vapor pressure deficit) during sampling and measurements are shown in table 1.

### Measurements

LA was determined after photocopying 25–35 leaves from each stand using the Interactive Binary System (IBAS). DW was determined after drying the leaves to a constant weight in a forced-air oven at 60 °C. LMA, and its components FW/LA and DW/FW as indicators of thickness and density, respectively (Dijkstra, 1989), were calculated.

### Mineral content

The mineral content of the leaves was determined on three replicates of dried material (25–35 leaves) ground to a fine powder in a Mixer-Mill 800 (Spex)

**Table 1.** Incident radiation (PAR), air temperature, leaf temperature and vapor pressure deficit (VPD) values during gas exchange measurements (1200–1400 hours).

	17 Feb	19 May	10 July	19 Sept	1 Dec
PAR (μmol.m <sup>-2</sup> .s <sup>-1</sup> )	1 563 ± 98	898 ± 60	1 613 ± 68	846 ± 63	1 635 ± 24
Air temp (°C)	21.7 ± 0.21	26.4 ± 0.16	30.9 ± 0.15	28.6 ± 0.19	18.7 ± 0.17
Leaf temp (°C)	23.2 ± 0.17	26.7 ± 0.26	32.8 ± 0.21	28.8 ± 0.29	20.9 ± 0.19
VPD (KPa)	1.93 ± 0.05	2.67 ± 0.10	3.84 ± 0.07	3.06 ± 0.09	1.83 ± 0.03

with balls of tungsten carbide. Total nitrogen and carbon concentrations were determined using gas chromatography (Nitrogen Analyzer 1500, Carlo Erba, Milan, Italy) in standard conditions (Pella et al, 1984). Phosphorus, potassium and calcium content were determined after humid digestion using inductively coupled plasma atomic absorption.

### Total soluble carbohydrates

Total soluble carbohydrates were determined according to Somogyi (1952). The carbohydrate content was based on the mean of three replicates obtained from 25–35 leaves per stand and sampling day.

### Rubisco activity

Ribulose biphosphate carboxylase (Rubisco) activity was determined using samples of 1 g from ten frozen leaves (collected at midday) of each stand which were cut into small pieces. Two replicates per day and stand were assayed. The enzymatic activity of the extract was measured, after full activation, by spectrophotometric end-point titration of D-PGA formed in a 60 s assay at 25 °C (Di Marco and Tricoli, 1983).

### Photosynthetic pigment

Photosynthetic pigment content was determined according to Lichtenthaler (1987).

### Gas exchange

Gas exchange measurements of net CO<sub>2</sub> assimilation rate, and leaf conductance to water vapor, were performed in situ in attached, fully expanded leaves of control plants and resprouts of burned and tree-felled stands using a portable open gas exchange system (LCA2, Analytical Development Company Ltd, Hoddesdon, Herts, UK). This measures both CO<sub>2</sub> and water vapor exchange using a differential mass balance approach (Field et al, 1989). Leaf temperature, absolute humidity of the air, and PAR were measured inside the cuvette. The leaf chamber was held normal to the solar beam and each measurement was carried out in less than 1 min. Conductance values can be affected by this gas exchange system

since there is no humidity control in the chamber, depending on the fluxes of leaf transpiration and injected dry air. As shown in table I, air and leaf temperatures were within 2 °C, suggesting that the lack of temperature regulation in the LCA-2 chamber did not cause overheating of the leaves. Measurements were taken between 1200 and 1400 hours local time. At least 12 replicates per stand were performed each day.

### Statistical analysis

Assuming that control, burned and tree-felled stands followed a normal distribution, we tested the equality of variances in the three stands. We found that they were the same and therefore stands could be compared and tests were carried out. For each parameter studied (ie, gas exchange, Rubisco activity, pigments, nutrients, leaf mass per area, carbohydrates and water content), the differences between measurement dates (time) and between the three groups of leaves (control, burned and tree-felled) at those dates were tested with two-way unbalanced ANOVA (Arenas et al, 1993) taking  $P \leq 0.05$  as level of significance. When significant differences appeared, another ANOVA test, using Bonferroni's methods, was applied ( $P \leq 0.01$ ).

## RESULTS

In our conditions, no significant differences in amount or trend were observed between the two kinds of resprout (originated after fire and after tree-fell, respectively) in any parameter measured.

### Gas exchange measurements

Net photosynthesis (fig 1a) was significantly different between control and resprouts only under high irradiance and temperature conditions and high VPD (table I). Resprouts showed higher photosynthetic rates (almost double) than control leaves during early and late summer. However, net photosynthesis was markedly depressed in all stands during

this period. Leaf conductance (fig 1b) was significantly higher (45%) in resprouts than in control leaves in all seasons except winter. The values remained constant throughout the year in resprouts.

### Rubisco activity

Ribulose biphosphate carboxylase (Rubisco) activity at midday was significantly higher in burned and tree-felled resprouts than in control leaves (fig 1c). Moreover, the Rubisco activity in resprouts showed a decreasing trend from winter to autumn, whereas in control leaves, no significant differences were observed throughout the year.

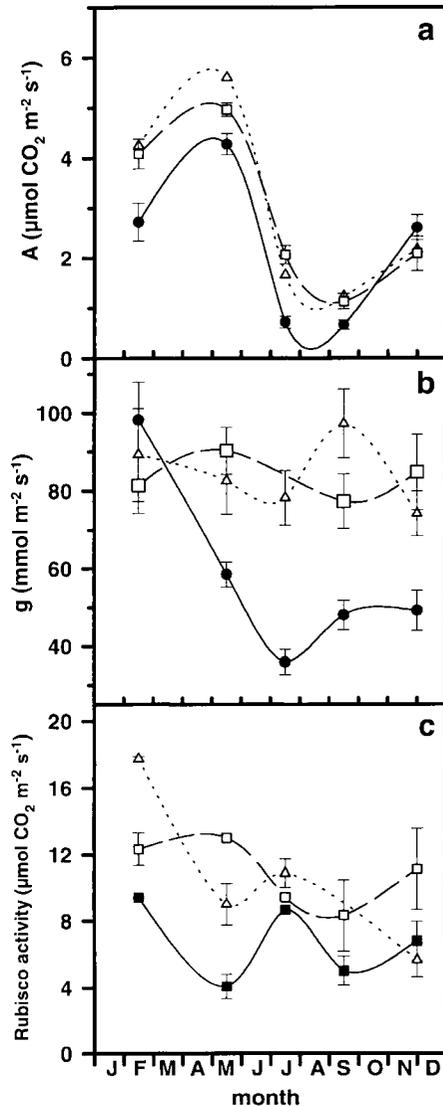
### Photosynthetic pigments

The resprouts originated after fire and tree-fell showed significantly higher total chlorophyll (a + b) content, on an area basis, than the original vegetation (fig 2a). Carotenoid contents on an area basis (fig 2c) also showed significant differences between stands (twice as high in resprouts as in control leaves) but not throughout the year. On a dry weight basis, neither total chlorophyll content (fig 2b) nor carotenoid content (fig 2d) were significantly different from controls.

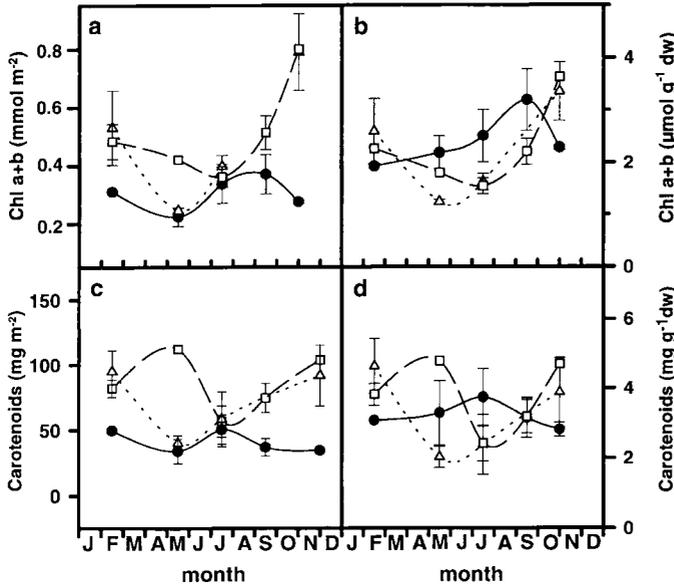
Increased soluble protein content and nitrogen content in these resprouts has already been reported by Fleck et al (1996). Considering the ratio Chl (a + b)/soluble protein, no significant differences were found between the stands or throughout the seasons.

### C, P, K and Ca content

C, P, K and Ca content of the leaves on a dry weight basis showed significant differ-



**Fig 1.** (a) Net photosynthesis (A); (b) leaf conductance (g); and (c) ribulose biphosphate carboxylase (Rubisco) activity in *Quercus ilex* leaves from control (●) burned (Δ) and felled (□) stands throughout 1 year following disturbance. Values of A and g are mean ± standard error (SE) for 12 replicates per stand and values of Rubisco are mean ± SE for two replicates from ten leaves.



**Fig 2.** Total chlorophyll (chl) content on area (a) and dry weight (dw) (b) basis, and carotenoid content on area (c) and dry weight (d) basis in *Quercus ilex* leaves from control (●), burned (Δ) and felled (□) stands throughout 1 year following disturbance. Values are mean  $\pm$  SE for two replicates from ten leaves.

ences throughout the year (table II). Significant differences between resprouts and control were observed in P (16% increase), K (27% decrease) and Ca (8% increase) content. On an area basis, the nutrient content was considerably higher in the resprouting vegetation: C content increased 82%; P, 118%; K, 30% and Ca, 95% in resprouts.

#### **Leaf mass per area (LMA)**

Higher values were observed in the resprouts (80%) with respect to control leaves (table III). Significant differences throughout the year were exhibited by resprouts and control leaves.

#### **The ratio of fresh weight to leaf area (FW/LA)**

FW/LA was significantly higher in resprouts than in control leaves, and seasonal varia-

tions in the three stands were observed. The values oscillated between 375 and 494 g FW.m<sup>-2</sup> for resprouts and 211 and 291 g FW.m<sup>-2</sup> for control.

#### **% Leaf dry weight**

% Leaf dry weight (DW/FW.100 or %DW) did not show significant differences between control and resprouts or throughout the year. The values were maintained around 53%.

#### **Total soluble carbohydrates (CH)**

CH on a dry weight basis, were significantly higher in resprouts in winter and autumn (table III). On an area basis, they were twice as high in resprouts as in control leaves. Significant differences were also observed in the three stands throughout the year on both bases. In resprouts, the values tended to increase from early summer.

**Table II.** C, P, K and Ca content (mg g<sup>-1</sup> DW) throughout the growing season for *Quercus ilex* leaves in control (C), burned (B) and felled (F) stands. Values are means  $\pm$  standard error (SE) of three replicates from 25–35 grounded leaves.

		C	P	K	Ca
Winter	C	503 $\pm$ 1.8 <sup>a</sup>	0.88 $\pm$ 0.01 <sup>a</sup>	5.67 $\pm$ 0.42 <sup>a</sup>	7.63 $\pm$ 0.30 <sup>a</sup>
	B	487 $\pm$ 2.7 <sup>a</sup>	1.33 $\pm$ 0.05 <sup>d</sup>	4.26 $\pm$ 0.29 <sup>d</sup>	8.05 $\pm$ 0.18 <sup>d</sup>
	F	494 $\pm$ 0.9 <sup>a</sup>	1.21 $\pm$ 0.03 <sup>d</sup>	4.29 $\pm$ 0.17 <sup>d</sup>	9.81 $\pm$ 0.54 <sup>d</sup>
Spring	C	497 $\pm$ 0.5 <sup>a</sup>	0.97 $\pm$ 0.01 <sup>a</sup>	6.33 $\pm$ 0.43 <sup>b</sup>	7.76 $\pm$ 0.58 <sup>b</sup>
	B	495 $\pm$ 0.3 <sup>a</sup>	1.21 $\pm$ 0.13 <sup>d</sup>	4.12 $\pm$ 0.21 <sup>d</sup>	8.65 $\pm$ 0.84 <sup>d</sup>
	F	493 $\pm$ 1.8 <sup>a</sup>	1.15 $\pm$ 0.05 <sup>d</sup>	4.16 $\pm$ 0.11 <sup>d</sup>	8.99 $\pm$ 0.32 <sup>d</sup>
Early summer	C	493 $\pm$ 1.9 <sup>a</sup>	0.92 $\pm$ 0.007 <sup>a</sup>	7.44 $\pm$ 0.08 <sup>c</sup>	11.76 $\pm$ 0.12 <sup>c</sup>
	B	499 $\pm$ 0.8 <sup>a</sup>	0.82 $\pm$ 0.03 <sup>e</sup>	4.65 $\pm$ 0.02 <sup>d</sup>	15.20 $\pm$ 1.88 <sup>e</sup>
	F	494 $\pm$ 1.5 <sup>a</sup>	1.53 $\pm$ 0.05 <sup>f</sup>	3.95 $\pm$ 0.07 <sup>d</sup>	10.55 $\pm$ 0.39 <sup>e</sup>
Late summer	C	485 $\pm$ 0.5 <sup>a</sup>	0.80 $\pm$ 0.03 <sup>d</sup>	6.57 $\pm$ 0.30 <sup>b</sup>	6.83 $\pm$ 1.68 <sup>b</sup>
	B	506 $\pm$ 0.9 <sup>b</sup>	0.73 $\pm$ 0.01 <sup>b</sup>	4.23 $\pm$ 0.13 <sup>d</sup>	9.93 $\pm$ 1.26 <sup>c</sup>
	F	513 $\pm$ 0.7 <sup>b</sup>	0.87 $\pm$ 0.01 <sup>b</sup>	5.20 $\pm$ 0.06 <sup>d</sup>	8.48 $\pm$ 0.94 <sup>e</sup>
Autumn	C	446 $\pm$ 0.9 <sup>c</sup>	1.00 $\pm$ 0.02 <sup>c</sup>	4.48 $\pm$ 0.06 <sup>d</sup>	10.05 $\pm$ 0.78 <sup>c</sup>
	B	449 $\pm$ 2.5 <sup>c</sup>	0.90 $\pm$ 0.005 <sup>c</sup>	4.66 $\pm$ 0.15 <sup>d</sup>	8.01 $\pm$ 0.74 <sup>d</sup>
	F	451 $\pm$ 1.3 <sup>c</sup>	0.89 $\pm$ 0.05 <sup>c</sup>	4.32 $\pm$ 0.48 <sup>d</sup>	7.19 $\pm$ 0.52 <sup>d</sup>

abcde Values with the same superscript letter are not significantly different.

**Table III.** Leaf mass per area (LMA; g DW.m<sup>-2</sup>) and total soluble carbohydrates (CH; g gluc g<sup>-1</sup> DW) throughout the growing season for *Quercus ilex* leaves in control, burned and felled stands. LMA values are means  $\pm$  standard error (SE) of 25–35 leaves. CH values are means  $\pm$  SE of three replicates from 25–35 grounded leaves.

	Control		Burned		Felled	
	LMA	CH	LMA	CH	LMA	CH
Winter	161 $\pm$ 8 <sup>a</sup>	0.08 $\pm$ 0.001 <sup>a</sup>	204 $\pm$ 5 <sup>c</sup>	0.10 $\pm$ 0.005 <sup>c</sup>	213 $\pm$ 5 <sup>c</sup>	0.11 $\pm$ 0.005 <sup>c</sup>
Spring	102 $\pm$ 5 <sup>b</sup>	0.09 $\pm$ 0.007 <sup>a</sup>	197 $\pm$ 14 <sup>c</sup>	0.08 $\pm$ 0.005 <sup>a</sup>	233 $\pm$ 7 <sup>c</sup>	0.10 $\pm$ 0.002 <sup>a</sup>
Early summer	134 $\pm$ 4 <sup>a</sup>	0.10 $\pm$ 0.003 <sup>a</sup>	244 $\pm$ 6 <sup>d</sup>	0.10 $\pm$ 0.005 <sup>a</sup>	233 $\pm$ 8 <sup>d</sup>	0.12 $\pm$ 0.005 <sup>a</sup>
Late summer	116 $\pm$ 7 <sup>a</sup>	0.08 $\pm$ 0.007 <sup>a</sup>	278 $\pm$ 3 <sup>d</sup>	0.11 $\pm$ 0.007 <sup>a</sup>	233 $\pm$ 26 <sup>d</sup>	0.07 $\pm$ 0.002 <sup>a</sup>
Autumn	121 $\pm$ 4 <sup>a</sup>	0.09 $\pm$ 0.006 <sup>a</sup>	236 $\pm$ 1 <sup>d</sup>	0.13 $\pm$ 0.004 <sup>b</sup>	220 $\pm$ 19 <sup>d</sup>	0.12 $\pm$ 0.004 <sup>b</sup>

abcd Values with the same superscript letter are not significantly different.

## DISCUSSION

The physiological characteristics of the resprouting vegetation were significantly different from the original vegetation and enhanced photosynthesis (fig 1a) and growth, as already observed after fire by, among others, Schlesinger and Gill (1980) in California.

Differences between kinds of resprout (after fire and after tree-fell) were not observed in any parameter measured although differences in nutrient availability were thought to occur as reported by Oechel and Hastings (1983) and Hastings et al (1989) in chaparral shrub species after burning or hand-clipping.

In our study, resprouts were especially efficient under stressful conditions which occur in a Mediterranean climate in the summer at high temperature, irradiance and VPD (table I). Kruger and Reich (1993) reported an apparent differential leaf sensitivity to leaf-to-air vapor pressure gradient between controls and resprouts after coppicing. Higher water availability to the growing resprouts due to a greater root-to-shoot ratio (De Souza et al, 1986; Saruwatari and Davis, 1989) or to higher soil-to-leaf hydraulic conductivity (Kruger and Reich 1993), allowed leaf conductance to remain higher and constant throughout the growing season, even in the summer, in contrast to the original vegetation (fig 1b).

Increased leaf conductance in burned plots with respect to unburned plots in hot seasons has been reported by Busch and Smith (1983), Knapp (1985), Hastings et al (1989) and Reich et al (1990) among others, and by our group in *Arbutus unedo* resprouts after wildfire (Fleck et al, 1995).

Although it has sometimes been related to an increase in plant water potential, it is still controversial whether soil water, leaf water content (Gollan et al, 1985) or hydraulic conductivity (Meinzer and Grantz, 1990) controls maximum leaf conductance.

In our study, the lack of differences in nutrients and carbohydrates concentration between resprouts after fire and tree-fell (tables II and III) indicates that with respect to controls, their values were a consequence of higher availability to the reduced shoot, independently of those released by the action of fire. It should be mentioned that some of the soluble nutrients deposited in the ash may be lost by erosion if not immediately absorbed (De Bano and Conrad, 1978). The results suggest the importance of underground organs such as lignotubers and burls during the early stages of development as sites of carbohydrate and nutrients enhancing shoot elongation, as described by Malanson and Trabaud (1988) and Mesleard and Lepart (1989) after disturbances.

Resprouts always showed significantly higher nutrient and carbohydrate content with respect to control when the values were considered on an area basis, due to the higher LMA in resprouts (table III).

The two components of LMA, thickness (FW/LA) and leaf density (%DW), varied independently, as reported by Witkowski and Lamont (1991) on several sclerophyllous species. We observed that resprouts differed from controls only in their greater thickness.

The higher Rubisco activity in resprouts (fig 1c) enables them to achieve higher photosynthesis rates than controls. Higher photosynthetic capacity is predictable since it is highly correlated with leaf N content (Evans and Seemann, 1989), which was higher in resprouts.

Nevertheless, *Q ilex*, like Californian evergreen trees or Australian sclerophylls, showed high N content and low photosynthetic rates in all the stands. This could be related to larger investment of N in structures for longevity (Field and Mooney, 1986).

N investment in thylakoids (chlorophylls) or in Rubisco and other CO<sub>2</sub> processing

enzymes was not different in resprouts and controls since we did not observe significant differences between their chlorophyll/soluble protein ratio.

Increased carotenoids in resprouts (fig 2c) may contribute to a higher protection against photoinhibitory processes described in Mediterranean species (Demmig-Adams et al, 1989; Quick et al, 1992). Nevertheless, since its content did not change seasonally it may not be enough to avoid, but merely attenuate the summer midday depression of photosynthesis in spite of stomatal opening maintenance and higher Rubisco activity.

## ACKNOWLEDGMENTS

This work has been supported by funds from CICYT (NAT 90-0350). We wish to thank Dr C Arenas for helpful discussions on the statistical treatment, S Benitez, J Sabat and 'Servicios Científico Técnicos Universidad de Barcelona' for technical assistance and R Rycroft for correcting the English text.

## REFERENCES

- Arenas C, Cuadras CM, Fortiana J (1993) Multicua. Paquete no standard de análisis multivariante. *Publicaciones Depto Estadística*, Barcelona, Spain, 1-80
- Björkman O (1981) Responses to different quantum flux densities. In: *Physiological Plant Ecology. I. Responses to the Physical Environment. Encyclopedia of Plant Physiology* (QL Lange, PS Nobel, CB Osmond, Z Ziegler, eds), Springer, Berlin, Heidelberg, New York, new series, vol 12 A, 57-107
- Busch DE, Smith SD (1993) Effects of fire on water and salinity relations of riparian woody taxa. *Oecologia* 94, 186-194
- Castell C (1992) Ecofisiologia d'individus adults i rebrots de dues espècies escleròfil·les mediterrànies: *Arbutus unedo* i *Quercus ilex*. PhD Thesis, Autonomous University of Barcelona, Spain
- Christensen NL, Muller CG (1975) Effects of fire on factors controlling plant growth in *Adenostoma* chaparral. *Ecol Monogr* 445, 29-55
- Correia MJ, Chaves MM, Pereira JS (1990) Afternoon depression in photosynthesis in grapevine leaves – evidence for a high light stress effect. *J Exp Bot* 41, 4417-4426
- De Bano LF, Conrad CE (1978) The effect of fire on nutrients in a chaparral ecosystem. *Ecology* 59, 489-497
- Demmig-Adams B, Adams WW III, Winter K, Meyer A, Schreiber U, Pereira JS, Kruger A, Czygan FC, Lange OL (1989) Photochemical efficiency of photosystem II, photon yield of O<sub>2</sub> evolution, photosynthetic capacity, and carotenoid composition during the midday depression of net CO<sub>2</sub> uptake in *Arbutus unedo* growing in Portugal. *Planta* 177, 377-387
- De Souza J, Silka PA, Davis SD (1986) Comparative physiology of burned and unburned *Rhus laurina* after chaparral wildfire. *Oecologia* 71, 63-68
- Dijkstra P (1989) Cause and effect of differences in specific leaf area. In: *Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants* (H Lambers et al, eds), SPB Academic Publishing, The Hague, The Netherlands, 125-140
- Di Marco G, Tricoli D (1983) RuBPCarboxilase determination by enzymic estimation of D-3-PGA formed. *Photosynth Res* 4, 145-149
- Evans JR, Seemann JR (1989) The allocation of protein nitrogen in the photosynthetic apparatus: costs, consequences, and control. In: *Photosynthesis* (WR Briggs, ed), Liss AR Inc, New York, 183-205
- Field C, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. In: *On the Economy of Plant Form and Function* (TJ Givnish, ed), Univ Press, Cambridge, 25-55
- Field C, Ball JT, Berry JA (1989) Photosynthesis: principles and field techniques. In: *Plant Physiological Ecology* (RW Pearcy, J Ehleringer, HA Mooney, PW Rundel, eds), Chapman and Hall, London, New York, 209-253
- Fleck I, Iñiguez F, Díaz C, Pascual M (1990) Effects of fire on photosynthesis and transpiration in a mediterranean ecosystem. In: *Current Research in Photosynthesis*, vol IV (M Baltscheffsky, ed), Kluwer Academic Publishers, The Netherlands, 695-698
- Fleck I, Sanjosé M, Grau D, Vidal D (1992) The effects of fire and tree-fell on photosynthesis in *Quercus ilex* resprouts. In: *Research in Photosynthesis*, vol IV (N Murata, ed), Kluwer Academic Publishers, Dordrecht, Boston, London, 687-690
- Fleck I, Díaz C, Pascual M, Iñiguez FJ (1995) Ecophysiological differences between first-year resprouts after wildfire and unburned vegetation of *Arbutus unedo* and *Coriaria myrtifolia*. *Acta Oecologica* 16, 55-69
- Fleck I, Grau D, Sanjosé M, Vidal D (1996) Carbon isotope discrimination in *Quercus ilex* resprouts after fire and tree-fell. *Oecologia* 105, 286-292
- Gollan T, Turner NC, Schulze ED (1985) The response of stomata and leaf gas exchange to vapor pressure deficits and soil water content. III. In the sclerophyl-

- lous woody species *Nerium oleander*. *Oecologia* 65, 356-362
- Gulmon SL, Chu CC (1981) The effects of light and nitrogen on photosynthesis, leaf characteristics, and dry matter allocation in the chaparral shrub, *Diplacus aurantiacus*. *Oecologia* 49, 207-212
- Hastings JH, Oechel WC, Sionit N (1989) Water relations and photosynthesis of chaparral resprouts and seedlings following fire and hand clearing. In: *The California Chaparral – Paradigms Reexamined* (SC Keeley, ed), Natural History Museum of Los Angeles, CA, USA, 107-113
- Hulbert LC (1988) Causes of fire effects in tall grass prairie. *Ecology* 69, 46-58
- Knapp AK (1984) Post-burn differences in solar radiation, leaf temperature and water stress influencing production in a lowland tallgrass prairie. *Am J Bot* 71, 220-227
- Knapp AK (1985) Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. *Ecology* 66, 1309-1320
- Kruger EL, Reich PB (1993) Coppicing alters ecophysiology of *Quercus illex* saplings in Wisconsin forest openings. *Physiol Plant* 89, 741-750
- Lichthentaler HK (1987) Chlorophylls and carotenoids, the pigments of the photosynthetic biomembranes. In: *Methods in Enzymology* (R Douce, L Packer, eds), Academic Press, New York, 350-382
- Malanson GP, Traubad L (1988) Vigour of post-fire resprouting by *Quercus coccifera* L. *J Ecol* 76, 351-365
- Meinzer FC, Grant DA (1990) Stomatal and hydraulic conductance in growing sugarcane: stomatal adjustment to water transport capacity. *Plant Cell Environ* 13, 383-388
- Mesleard F, Lepart J (1989) Continuous basal sprouting from a lignotuber: *Arbutus unedo* L and *Erica arborea* L as woody Mediterranean examples. *Oecologia* 80, 127-131
- Nobel PS (1977) Internal leaf area and cellular CO<sub>2</sub> resistance: photosynthetic implications of variations with growth conditions and plant species. *Physiol Plant* 40, 137-144
- Oechel WC, Hastings SJ (1983) The effects of fire on photosynthesis in chaparral resprouts. In: *Ecological Studies*, Vol 43, *Mediterranean-Type Ecosystems: The Role of Nutrients* (FJ Kruger, DT Mitchell, JUM Jarvis, eds), Springer, New York, 274-285
- Pella E, Bedoni L, Colombo B, Giuzzi G (1984) Data analysis in elemental gas chromatography. *Anal Chem* 56, 2504-2509
- Quick WP, Chaves MM, Wendler R, David M, Rodrigues ML, Passarinho JA, Pereira JS, Adcock MD, Lee-good RC, Stitt M (1992) The effect of water stress on photosynthetic carbon metabolism in four species grown under field conditions. *Plant Cell Environ* 15, 25-35
- Radosevich SR, Conard SG (1980) Physiological control of chamise shoot growth after fire. *Am J Bot* 67, 1442-1447
- Reich PB, Abrams MD, Ellsworth DS, Kruger EL, Tabone TJ (1990) Fire affects ecophysiology and community dynamics of Central Wisconsin oak forest regeneration. *Ecology* 71, 2179-2190
- Reich PB, Walters MB, Ellsworth DS, Uhl C (1994) Photosynthesis-nitrogen relation in Amazonian tree species. I. Patterns among species and communities. *Oecologia* 97, 62-72
- Sabaté S (1993) Estructura i contingut de nutrients a les capçades de *Quercus illex* L del bosc de les muntanyes de Prades: ingerència de les condicions naturals de creixement i efecte de manipulacions experimentals. PhD Thesis, University of Barcelona, Spain
- Saruwatari MW, Davis SD (1989) Tissue water relation of three chaparral shrub species after wildfire. *Oecologia* 80, 303-308
- Schlesinger WH, Gill DS (1980) Biomass, production, and changes in the availability of light, water and nutrients during the development of pure stands of the chaparral shrub, *Ceanothus megacarpus* after fire. *Ecology* 61, 781-789
- Serrasolsas I (1994) Fertilitat de sòls forestals afectats pel foc. Dinàmica del nitrogen i del fòsfor. PhD Thesis, University of Barcelona, Spain
- Serrasolsas I, Alcañiz JM, Arias X, Josa R, Solé A, Vallejo VR (1992) The effects of burning and clear-cutting in forest floor layers of holm oak forest. In: *Responses of Forest Ecosystems to Environmental Changes* (A Teller, P Mathy, JNK Jeffers, eds), Elsevier Applied Science, London, New York, 641-642
- Somogyi M (1952) Notes on sugar determination. *Biol Chem* 195, 19-23
- Traubad L, Méthy M (1988) Modifications dans le système photosynthétique de repousses apparaissant après feu de deux espèces ligneuses dominantes des garrigues méditerranéennes. *Oecol Plant* 9, 229-243
- Tenhunen JD, Beyschlag W, Lange OL, Harley PC (1987) Changes during summer drought in leaf CO<sub>2</sub> uptake rates of macchia shrubs growing in Portugal: limitations due to photosynthetic capacity, carboxylation efficiency and stomatal conductance. In: *Plant Response to Stress. Functional Analysis in Mediterranean Ecosystems* (JD Tenhunen, OL Catarino, WC Oechel, eds), NATO ASI Series, Series G, Springer, Berlin, 305-327
- Thomas CM, Davis SD (1989) Recovery patterns of three chaparral shrubs species after wildfire. *Oecologia* 80, 309-320
- Witkowski ETF, Lamont BB (1991) Leaf specific mass confounds leaf density and thickness. *Oecologia* 88, 486-493