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Optimization of carbon gain in canopies of Mediterranean evergreen oaks

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Summary — The main goal of this study was to analyze the depth-distribution of leaf mass per area (LMA) measured in ten canopies of Mediterranean evergreen oaks, five canopies of *Quercus coccifera* and five canopies of *Q ilex*, across soil water availability gradients in southern France, Spain and Portugal. There was a significant site effect on LMA with values being lower in mesic sites compared to those on xeric sites. In all canopies, LMA decreased by up to 50% from the top to the bottom. The relationships between cumulative leaf area index and LMA could be represented by an exponential function. For two canopies of *Q ilex* growing in contrasting environments, we analyzed the interrelationships among LMA, mass-based nitrogen, mass-based metabolic versus structural (total fiber) content, photosynthetic electron transport and carbon isotope composition. There was no difference in mass-based nitrogen or fiber content among upper and lower canopy positions in both locations. The maximum quantum yield of linear electron flow can be considered to be constant within the canopy. The area-based maximal electron transport rate and the carbon isotope composition were significantly linearly related to the LMA. Finally, we tested whether the observed depth-distribution follows the pattern suggested by some optimization theories.

Mediterranean evergreen canopy / leaf mass per area / photosynthesis-related leaf property / *Quercus ilex / Quercus coccifera*

Résumé — Optimisation du gain de carbone par les canopées de chênes méditerranéens à feuillage persistant. *Le principal objectif de cette étude est d'analyser la distribution verticale de la masse surfacique foliaire (LMA) dans dix formations à chênes méditerranéens à feuillage persistant au sein de gradients de disponibilité en eau dans le sud de la France, en Espagne et au Portugal : cinq formations à* Quercus coccifera *et cinq à* Q ilex. *Le LMA varie significativement entre les sites. Les valeurs de LMA les plus faibles sont atteintes dans les sites les plus mésiques pour les deux espèces. Dans toutes les formations, le LMA décroît de plus de 50 % du sommet du couvert à sa base. Les relations entre l'indice foliaire cumulé et le LMA peuvent être décrites par des fonctions exponentielles. Pour deux formations à chênes verts poussant dans des environnements contrastés, nous avons analysé les interrelations entre le LMA, la teneur en azote et en fibre par unité de masse foliaire, le transport* *d'électrons photosynthétiques et la composition isotopique du carbone. Il n'y a pas de différence significative dans les teneurs en azote ou en fibres au sein du couvert. Le rendement quantique maximum du transfert linéaire d'électrons peut être considéré constant dans le couvert. Le transport maximal d'électrons par unité d'aire foliaire et la composition isotopique du carbone sont significativement linéairement reliés au LMA. Finalement, nous comparons les distributions verticales observées avec les patrons suggérés par les théories d'optimisation.*

***canopées de chênes méditerranéens / masse surfacique foliaire / propriétés photosynthétiques des feuilles /* Quercus ilex / Quercus coccifera**

INTRODUCTION

Canopies of Mediterranean-type ecosystems, and particularly those of evergreen oaks are spatially heterogeneous environments. Energy capture and carbon gain depend on both the photosynthetic responses of individual leaves and their integration into canopy. Structural and functional differences among leaves from different vertical positions have long been recognized and radiation levels are known to be influenced by canopy position (Oren et al, 1986; Givnish, 1988; Ashton and Berlyn, 1994). Many researchers have considered how canopies may organize leaf properties to maximize carbon gain (Field, 1983; Hirose and Werger, 1987; Chen et al, 1993). Their analyses have investigated how nitrogen, a resource known to be related to leaf photosynthetic capacity, should be allocated within the canopy. Similarly, other analyses have studied how should the total dry mass of leaves be distributed with depth (Gutschick et al, 1988).

Understanding how the canopies are organized and assessing vertical variation in leaf carbon assimilation should i) give information on how carbon and nitrogen resources are partitioned; and ii) provide relationships appropriate to scale up leaf level properties to canopy level. The objectives of this study were to: i) describe the pattern of the leaf mass per area within Mediterranean evergreen *Quercus coccifera* and *Q ilex* canopies from sun-exposed to shaded leaves; ii) test if patterns are species- or site-specific or both; iii) describe the extinction of other photosynthesis-related parameters within the canopies; and iv) compare morphological and physiological patterns with those predicted by some optimization theories.

MATERIALS AND METHODS

Study sites and sampling protocols

Components of the canopy architecture were measured: i) in four scrubs of monospecific *Q coccifera* L growing on hard to soft limestones, and ii) in two woodlands of *Q ilex* L growing on soils with contrasted water availability. Three *Q coccifera* stands were located in southern France along an elevational transect, ranging from La Palme (near sea level) to Saint-Martin-de-Londres (200 m above sea level), and the last near Murcia in southern Spain at Sierra de la Pila. These sites experience a wide range of climatic conditions (see Rambal and Leterme, 1987, for a more complete description). The two *Q ilex* stands were located in southern France at Puechabon and Montpellier-Camp-Redon (called further Camp-Redon), a xeric and a mesic site, respectively (Rambal, 1992). All stands were relatively even aged, all being 20–40 years old. The canopies were sampled in mid-July after the current-year foliage had fully expanded.

For *Q coccifera*, samples of foliage for determining the profiles of leaf area and the associated leaf mass per area (LMA) were obtained from five randomly located square columns of 1 m on a side that extended from the ground to the top of the canopy. All the foliage within the column was removed in 0.20 m increments from the top down by hand clipping, giving five to seven samples, each 0.20 m^3 volume. Leaf subsamples of approximately 100 leaves were taken from each sample. The areas of the fresh leaf subsamples were determined with a video leaf-area meter (Delta-T Image Analysis System, Delta-T Devices Ltd, UK). All the harvested leaves were dried at 65 °C for 24 h and weighed. Leaf area for each sample was calculated based on the LMA of the subsample and its total leaf dry mass.

For *Q ilex*, we estimated the leaf-area profiles with the LI-COR LAI-2000 plant canopy analyzer (LI-COR Inc, Lincoln, NE, USA). This instrument measures the gap fraction of the canopy based on diffuse blue light attenuation at five zenith angles simultaneously. Measurements were made at more than 20 locations in each stand to obtain a spatial average. Leaf area data were collected at each location at five vertical positions, ie, ground surface, and 1, 2, 3, and 4 m from the ground. At each location where the leaf area index measurement was taken or in its immediate vicinity, samples of approximately 100 leaves were taken for LMA determination (see above). In both stands, reference readings of sky brightness could be obtained quickly in sufficient large clearings nearby. Because direct sunlight on the canopy causes errors larger than 30% in the LAI-2000 measurements, we collected data on cloudy days. The calculated value at each height represents the leaf area above the sampling point (*L*).

For analysis and forthcoming developments, we will use LAI-*L*, ie, the cumulative leaf-area index measured from the ground. The LMA data were pooled into equidistant LAI-*L* classes and then averaged. We also included in this analysis published data on *Q coccifera* and *Q ilex* canopies in Portugal, France and Spain. The first set of data concerns a *Q coccifera* stand growing in a mesic location (see Rambal, 1992) at the Research Station of Quinta Sao Pedro near Lisbon (Portugal) and described by Tenhunen et al (1984). The second set came from the well-known 150-year-old *Q ilex* coppice of Le Rouquet in southern France (Eckardt et al, 1975). The last sets came from two sampling sites located in the Avic watershed near Prades (northeastern Spain) at the ends of an elevation gradient: at the bottom of the valley and near the ridge of the mountain. These two locations will be referred to as Valley and Ridge, respectively (Sala et al, 1994).

Biochemical and isotopic analysis

Leaf material for isotopic and biochemical analysis was collected on two dates (April 1991 and April 1994) at Camp-Redon and on one date (April 1994) at Puechabon from 1-year-old leaves of three neighboring *Q ilex* trees within each locations. The leaves, after LMA determination, were ground to a fine powder, and analyzed for their carbon isotope composition relative to the Pee Dee Belemmite (PDB) standard, at the Service central d'analyse du CNRS, Vernaison, France. Long-term estimates of the intercellular CO_2 concentration within the leaf (C_i) were calculated by rearranging the equations originally developed by Farquhar et al (1982) as

$$C_i = C_a\,(\delta^{13}C_{air} - \delta^{13}C_{leaf} - a)/(b - a) \qquad [1]$$

where $\delta^{13}C_{air}$ and $\delta^{13}C_{leaf}$ are the carbon isotope compositions of the air and leaf, respectively, C_a is the CO_2 concentration in the atmosphere, *a* is the ^{13}C fractionation due to diffusion (4.4‰), and *b* is the net fractionation due to carboxylation (27‰). The water-use efficiency (A/E, or the molar ratio of photosynthesis A to transpiration E) is also related to C_i and C_a by:

$$A/E = (C_a - C_i)/(1.6\Delta w) \qquad [2]$$

where Δw is the leaf-to-air vapor pressure gradient.

Biochemical analysis was performed on the April 1994 samples only for the Camp-Redon and Puechabon locations. The nitrogen and fiber content of the leaves were determined using near-infrared reflectance spectroscopy (see Joffre et al, 1992 for a detailed description of the procedure). All samples were scanned with an NIR System 6500 spectrophotometer. The database used to build calibration equations comprises leaves of *Quercus* spp collected by us throughout all the French Mediterranean area and includes part of the database of Meuret et al (1993). The concentration of nitrogen (N) and total fiber of the calibration set samples were determined using wet chemistry methods. N was determined with a Perkin Elmer elemental analyzer (PE 2400 CHN) and total fiber (neutral detergent fiber, ie, hemicellulose + cellulose + lignin) was determined using the Fibertec procedure (Van Soest and Robertson, 1985). This allowed N and total fiber content (%) in the leaves to be determined from the spectra, using modified partial least squares regression with a standard error of prediction of 0.11% for nitrogen and 1.36% for total fiber.

Efficiency of linear electron transport

We also analyzed the variation within the canopy of electron-transport rates on sunlit, penumbral and shaded leaves of *Q ilex* in the Camp-Redon location. Fluorescence measurements were done in late winter on 1-year-old attached leaves at ambient temperature (ca 18 °C). The saturation pulse method associated with pulse amplitude modulation technique (Schreiber and Bilger, 1987) was used (fluorometer PAM-2000, Walz, Germany). The photochemical quantum efficiency of non-cyclic electron transport ($\Delta F/F_m'$) under increasing photosynthetic photon flux density (PPFD) (I) was measured according to Genty et al (1989). Actinic light was applied with a 20 W external halogen lamp (2050-H, Walz, Germany) providing I adjustable up to 2 000 μmol m^{-2} s^{-1}. The stability of the spectral distribution of photosynthetically active radiation was achieved by appropriate optical filters. The electron transport rate (J) was calculated assuming that one electron requires absorption of two quanta:

$$J = 0.5a\, I\, \Delta F/F_m' \qquad [3]$$

In order to calculate the absorbtance (a), transmittance and reflectance of leaves for the light source and the sun were measured with an integrating sphere on a spectrophotometer (Beckmann 5240). The relationships between J and I were adjusted according to Smith (1937):

$$J = \alpha\, I/(1 + \alpha^2 I^2/J_{max}^2)^{1/2} \qquad [4]$$

α being the maximum quantum yield of linear electron flow, J_{max} being the light-saturated rate of total non-cyclic electron transport in μmol m^{-2} s^{-1}.

RESULTS

Leaf mass per area varied continuously through the canopies from upper to lower canopy position and values at the top were two to three times greater than at the bottom of the canopy. For all the available data on the five *Q coccifera* and five *Q ilex* locations, the relationships between LMA and the cumulative leaf area index, LAI-*L*, were described by a two-parameter exponential relationship:

$$\mathrm{LMA} = \mathrm{LMA}_0\, e^{k_l(\mathrm{LAI}-L)} \qquad [5]$$

LMA_0 is the LMA of leaves with LAI-L = 0, ie, the LMA of the shaded leaves. k_l is the rate constant. We chose this equation in order to easily compare k_l with the extinction coefficients of models describing the distribution of solar radiation within plant canopies. For all sites, the relationships were significant to highly significant (see tables I and II).

For the *Q coccifera* locations, LMA_0 ranged from 110 g m^{-2} at Quinta Sao Pedro (Portugal) to 168 g m^{-2} at Sierra de la Pila (Southern Spain). The k_l values were between 0.127 and 0.294, values obtained respectively in these two locations. For the southern France locations, because of low intersite variation, the data were pooled and only one relationship was calculated with LMA_0 and k_l of 135 g m^{-2} and 0.201, respectively (see table I and fig 1a). We observed a gradient of the LMA_0 and the associated k_l from mesic area in Portugal to the most xeric site in southern Spain. This gradient was associated with a large decrease in leaf area index from 4.4 to 1.5.

For the *Q ilex* locations, LMA_0 ranged from 95 g m^{-2} at Camp-Redon (southern France) to 143 g m^{-2} at the Ridge location of the Prades watershed (northeastern Spain). The k_l values were between 0.088 and 0.251, values obtained at the Valley location of the Prades watershed (northeastern Spain) and in Puechabon (southern France), respectively (table II and fig 1bd). We found no clear link between LMA_0 and k_l values as for the *Q coccifera* canopies, but local variations of the site water balance induced local variation of both parameters. Hence, at the two Prades watershed canopies, we observed an

Table I. Parameters of the relationship between LMA and cumulated leaf-area index for some *Q coccifera* canopies.

Location	*LMA$_0$*	k	R^2	*LAI*	*Reference*
Saint-Martin-de-Londres, southern France	138	0.175	0.96	2.7	This study
Montbazin-Gigean, southern France	132	0.224	0.83	2.4	This study
La Palme, southern France	134	0.211	0.93	2.1	This study
Southern France (mean value)	135	0.201	0.87		This study
Sierra de la Pila, southern Spain	168	0.294	0.91	1.5	This study
Quinta Sao Pedro, Portugal	110	0.127	0.91	4.0	Tenhunen et al, 1984

LMA$_0$ is the LMA of shaded leaves (g m^{-2}). *k* is the rate constant of the LMA profile. *R*^{2} is the determination coefficient. LAI is the leaf area index of the whole-canopy.

Table II. Parameters of the relationship between leaf mass per area LMA and cumulated leaf area index for some *Q ilex* canopies.

Location	*LMA$_0$*	*k*	*R*^{2}	*LAI*	*Reference*
Camp-Redon, southern France	95	0.222	0.97	4.0	This study
Puechabon, southern France	130	0.251	0.90	2.9	This study
Le Rouquet, southern France	115	0.112	0.94	4.4	Eckardt et al, 1975
Prades Watershed (Valley), northeastern Spain	135	0.088	0.80	5.3	Sala et al, 1994
Prades Watershed (Ridge), northeastern Spain	143	0.100	0.87	4.6	Sala et al, 1994

LMA$_0$ is the LMA of shaded leaves (g m^{-2}). *k* is the rate constant of the LMA profile. *R*^{2} is the determination coefficient. LAI is the leaf area index of the whole-canopy.

increase of LMA$_0$ and k_l from the most mesic situation of the Valley location to the xeric Ridge location, this change being associated with a decrease of the leaf area index from 5.3 to 4.6. For the site with low soil water availability of Puechabon, the rate constant was 0.251, a value slightly lower than that observed in the driest location of *Q coccifera* in southern Spain (k_l = 0.294).

The relationships between the mass-based nitrogen and total fiber or structural contents and the LMA obtained for the Puechabon and Camp-Redon sites were shown on fig 2a–d. The slopes of linear regressions were close to zero (table III). Consequently, we can assume that the mass-based nitrogen and total fiber contents were constant within the canopies in both locations. The corresponding mean values were 1.58% (SE = 0.008%) and 1.39% (SE = 0.012%) for mass-based nitrogen contents and 64.9% (SE = 0.32%) and 57.1% (SE =

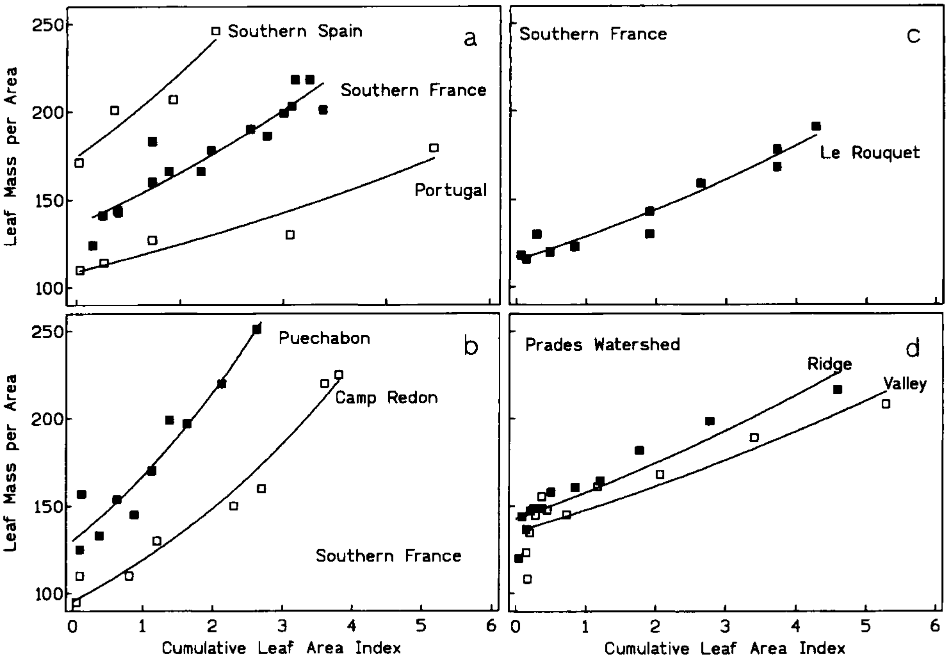

Fig 1. Profiles of LMA, the distribution of leaf mass per area in g m^{-2} according to the cumulate leaf area index in the canopy. Cumulative leaf-area index is plotted from the bottom of the canopy as LAI-*L*: **a)** *Q coccifera* canopies; the data from southern France are pooled in only one relationship; **b, c** and **d)** *Q ilex* canopies at Camp-Redon, Puechabon, Le Rouquet (southern France), and in two locations in the Avic watershed (northeastern Spain).

0.49%) for mass-based total fiber contents at Camp-Redon and Puechabon, respectively.

For Camp-Redon, we observed that the maximum quantum yield of linear electron flow, α, was not significantly related to the leaf mass per area (table III). Hence, it can be considered constant throughout the canopy. The corresponding mean value was 0.270 mol electron mol^{-1} quanta (SE = 0.006), ie, 0.270/4 = 0.0675 mol CO_2 mol^{-1} quanta assuming i) 90% leaf absorption; and ii) that only four electrons are used per CO_2 fixed. Area-based maximal electron transport rate was highly significantly related to LMA (fig 3 and table III). The slope of the curve was 0.157 resulting in an increase of this rate from 74.4 to 94.8 µmol m^{-2} s^{-1} followed an increase of LMA from 95 to 225 g m^{-2}.

The relationships between $\delta^{13}C_{leaf}$ and LMA were highly significant (table III and fig 4a,b). For Camp-Redon the slopes were 0.0296 and 0.0302 for the 1990 and 1993 leaves, respectively. These slopes were not significantly different and shown a temporal persistence. Assuming that $\delta^{13}C_{air}$ = –8.0‰ for the ambient atmospheric CO_2, the C_i/C_a (eq 1 and table III) decreased from 0.859 to 0.682 and from 0.827 to 0.648 when the LMA increased from 95 to 225 g m^{-2} for these 2 years, respectively. The slope of the relationships between $\delta^{13}C_{leaf}$ and LMA is slightly lower for Puechabon (0.0207) than for Camp-Redon.

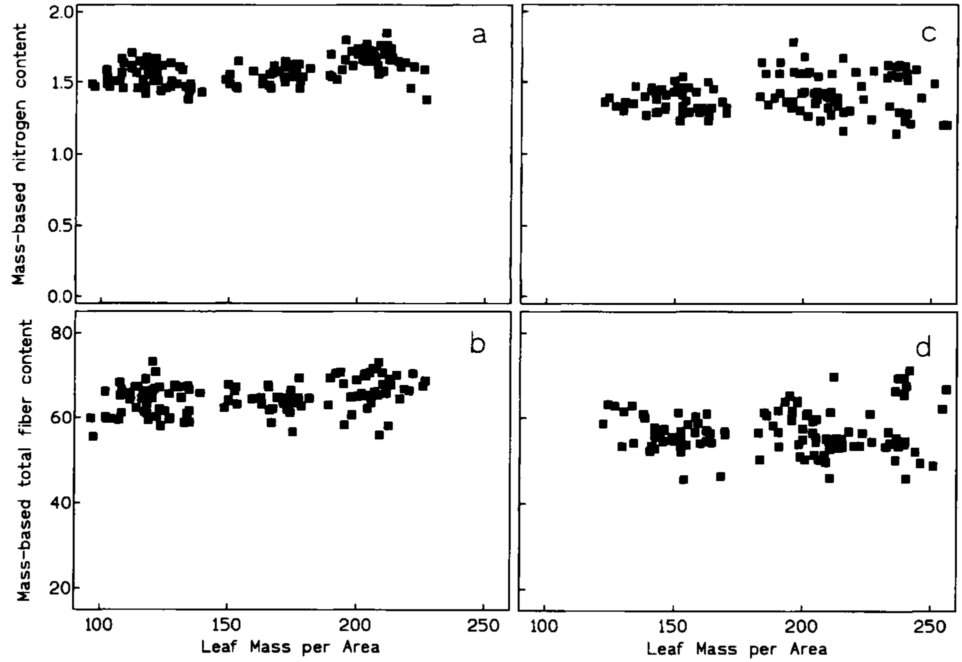

Fig 2. Relationships between mass-based nitrogen and total fiber contents, expressed in percent, and leaf mass per area, in g m^{-2}, for two *Q ilex* canopies in southern France, Camp-Redon (**a** and **b**) and Puechabon (**c** and **d**).

Table III. Summary of relationships between leaf mass per area (LMA) and some other leaf variables.

Location	*Dependent variable*	*Independent variable*	*Regression equation*	n	R^2
Camp-Redon	Mass-based nitrogen content	LMA	$y = 1.45 + 0.00085x$	130	0.15***
	Mass-based total fiber content	LMA	$y = 60.8 + 0.026x$	130	0.09***
	α	LMA		19	ns
	*J*max	LMA	$y = 59.5 + 0.157x$	19	0.42***
	$\delta^{13}C$ (1990 leaves)	LMA	$y = -33.9 + 0.0296x$	20	0.89***
	$\delta^{13}C$ (1993 leaves)	LMA	$y = -33.3 + 0.0302x$	18	0.80***
Puechabon	Mass-based nitrogen content	LMA		118	ns
	Mass-based total fiber content	LMA		118	ns
	$\delta^{13}C$ (1993 leaves)	LMA	$y = -32.4 + 0.0207x$	14	0.75***

Equations are given for least-square linear regressions. Mass-based nitrogen and fiber contents are expressed in g g^{-1}. The maximum quantum yield of linear electron flow (α) and the area-based maximal electron transport rate (J_{max}) are expressed in mol mol^{-1} and µmol m^{-2} s^{-1}, respectively; $\delta^{13}C$ is the carbon isotope composition; ‰; *n* is the sample size; R^2 is the determination coefficient. Not significant regression relationships are not presented. Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.01$ and ns not significant.

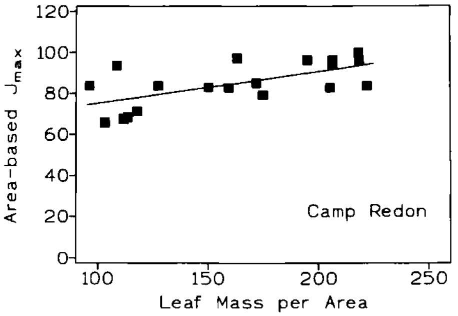

Fig 3. Relationship between area-based maximal electron transport rate at ambient temperature, expressed in µmol m^{-2} s^{-1}, and leaf mass per area, in g m^{-2}, for the *Q ilex* canopies of Camp-Redon (southern France).

DISCUSSION AND CONCLUSIONS

Vertical profiles of leaf properties within canopies

Givnish (1988) emphasized that for photosynthesis and respiration "expressing leaf parameters as a function of leaf mass may be more useful in assessing adaptation to light level than expressing them as a function of leaf area". In our study, all vertical variation in area-based nitrogen content or fiber could be explained by variation in LMA alone. This result is consistent with those obtained by Hollinger (1984) for the Californian evergreen oak *Q agrifolia*. He wrote: "It is unclear why the gradient in leaf N concentration is weak or absent". Sabaté et al (1995) observed a slight decrease from top to bottom of the canopy for the two *Q ilex* locations of the Prades watershed.

At Camp-Redon, the area-based J_{max} of sunlit leaves was 94.8 µmol m^{-2} s^{-1} (LMA = 225 g m^{-2}). From leaf photosynthesis measurements, Harley et al (1986) and Tenhunen et al (1987) obtained values of about 120–130 µmol m^{-2} s^{-1} for three evergreen Mediterranean oak species, *Q coccifera*, *Q suber* and *Q ilex*. Hollinger (1984) reported value of 139 µmol m^{-2} s^{-1} for *Q agrifolia*. In Wullschleger's (1993) synthesis concerning 109 C_3 plant species, the maximum rate of electron transport ranged from 17 to 372 µmol m^{-2} s^{-1} and averaged 134 µmol m^{-2} s^{-1} across all species. On an area basis, maximal electron transport rate of a shade leaf is less than of leaves exposed to full sunshine. Conversely, on a mass basis, transport rate of sunlit leaves is less than of leaves growing in shaded positions. Maximum quantum yield of linear electron flow do not show significant vertical variation within the canopy. It is almost independent

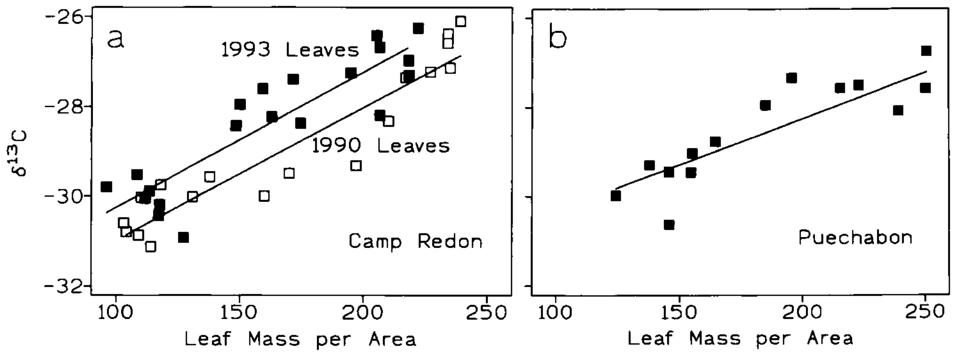

Fig 4. Relationships between the carbon isotope composition, in ‰, and leaf mass per area, in g m^{-2}, for two *Q ilex* canopies in Southern France, Camp-Redon (**a**): 1990 leaves and 1993 leaves, and Puechabon (**b**): 1993 leaves.

of leaf parameters, even of species (Björkman and Demmig, 1987).

The increasing foliar $\delta^{13}C$-values with LMA found in our study (fig 4) are consistent with observations from other forest canopies showing an increase of $\delta^{13}C$-values with height in trees (Ehleringer et al, 1986; Schleser, 1990; Garten and Taylor, 1992; Waring and Silvester, 1994). Changes in foliar $\delta^{13}C$ within the canopy may arise as a result of two dissimilar processes: i) vertical discrimination due to change in stomatal conductance or carboxylation leading to changes in C_i/C_a ratios; and ii) within-canopy gradients in the $\delta^{13}C$-value of atmospheric CO_2. Like Ehleringer et al (1986), we assumed "a small component of the change in leaf carbon isotope composition to be due to source difference" and will further be attributed to change in C_i.

The continuous nature of the change in many leaf parameters within the canopy suggests that separation into sunlit and shaded foliage classes is arbitrary. Photosynthetic characteristics such as PPFD response parameters typically vary along a gradient from sun to shade such as is found in evergreen (Hollinger, 1989) or deciduous (Ellsworth and Reich, 1993; Hamerlynck and Knapp, 1994) forest canopies, and in orchard trees (DeJong and Doyle, 1985). They showed that leaves from the top of the canopy have higher rates of assimilation per unit of leaf area and become saturated at higher PPFD than those from the bottom of the canopy. These observations suggest that the photosynthetic apparatus at different levels in the canopy is adapted to the prevailing light conditions. At the northern limit of the distribution area of *Q ilex*, Wagner et al (1991) showed that area-based light-saturated photosynthesis, compensation point and dark respiration decreased continuously from upper (LMA = 216 g m^{-2}) to lower canopy positions (LMA = 90 g m^{-2}). There were no significant differences in mass-based light-saturated photosynthetic rate. Meister et al (1986) presented similar results for two *Quercus coccifera* canopies by comparing photosynthetic properties of sunlit and lowermost shade leaves. In *Q ilex* canopies, the area-based leaf chlorophyll content was relatively constant among different level in the canopy (Gratani and Fiorentino, 1986). Consequently, mass-based chlorophyll increased in progressively deeper levels in the canopy. This increase in leaf chlorophyll per mass with increasing shading reflects the high plasticity of investments into light-harvesting capacity (see Lewandowska et al, 1976; Evans, 1989). Further studies will be necessary to understand organization of the photosynthetic apparatus under various conditions of irradiance and clarify the interrelationships between electron transport capacity, chlorophyll and nitrogen contents. LMA has also been correlated to vary with the activity of the enzyme RuBP carboxylase (Bowes et al, 1972). For practical use such structural characteristics must be easily measured and correlated, not necessarily functionally related, with biochemical-physiological processes (see Oren et al, 1986; Ellsworth and Reich, 1993).

Photosynthetic acclimation (see Evans, 1993) is expected to result in lower canopy leaves. These leaves can be characterized by low light-saturated photosynthetic rate per unit area and dark respiration but high chlorophyll contents thereby reducing the maintenance cost while increasing light-capturing capabilities. Acclimation of the photosynthetic apparatus also typically involves a trade-off in the relative importance of carbon-fixing and light harvesting components and likely N partitioning among these two components (see further Chen et al, 1993). This division is convenient because it functionally represents the reactions of photosynthesis which can be transposed into the photosynthetic model of Farquhar and Von Caemmerer (1982). It is interesting to discuss these results in the light of some optimization theories developed to analyze the vertical patterns of leaf parameters. We will distinguish here two major theory classes, those based on the optimization of the distribution of nitrogen, and those based on optimization of the distribution of the LMA.

Some optimization theories

Using an econometric model, Mooney and Gulmon (1979) predicted that decreasing PPFD availability should decrease the level of photosynthetic proteins. Consequently, carbon gain for a whole-canopy should be maximized when leaf nitrogen is distributed in leaves that receive the highest PPFD, which have the highest nitrogen content. On this basis, Field (1983) developed a biochemically based model of leaf photosynthesis, derived from works of Farquhar and Von Caemmerer (1982), to predict the 'optimal' distribution of leaf nitrogen content that maximizes daily photosynthetic carbon gain over a canopy of a Mediterranean drought-deciduous shrub. In this model, maximum carboxylation rate and electron-transport are related with mass-based leaf nitrogen content. From the simulation results, he ranked three possible nitrogen distributions: optimal, uniform and actual. The expected daily net photosynthesis was greater with the optimal than with the measured nitrogen distribution, but greater with the measured than with the uniform distribution. With a similar optimization perspective, Hirose and Werger (1987) suggested that, given a fixed amount of nitrogen available to leaves, plants optimize total whole-canopy photosynthesis. They proposed that decreasing area-based leaf nitrogen content with depth tends to maximize total daily photosynthesis carbon gain. The original model of Hirose and Werger (1987) assumed a linear dependence on leaf nitrogen content of both the apparent quantum yield for CO_2 assimilation and the curvature factor of the photosynthesis–PPFD response curve of the three-parameter model of Johnson and Thorley (1984). As a consequence, the optimal leaf distribution will depend only on the extinction of PPFD. The nitrogen allocation pattern predicted by this model is similar to, although less uniform than, their observed patterns. The observed rate constant (or the coefficient of nitrogen allocation) of the exponential curve is less than the optimum. Chen et al (1993) developed a coordination theory. They hypothesized that plants allocate nitrogen in such a way as to maintain a balance between the Rubisco-limited rate of carboxylation and the electron transport-limited rate of carboxylation. In the model, maximum carboxylation rate and maximum electron transport are linearly related to area-based nitrogen content. The nitrogen distribution obtained using the coordination theory is always slightly more uniform than those obtained using optimization theory of Hirose (ie, coordinated rate constant < optimal rate constant).

Gutshick and Wiegel (1988) propose to answer the question: "Given the total dry mass of leaves in a canopy per unit of ground area, how should this mass be distributed with depth to maximize the photosynthetic rate of the canopy?" That is, how should the LMA vary with cumulative-leaf-area index? The general assumptions underlying their model were the same as in Hirose and Werger (1987): "The greatest photosynthetic capacity and corresponding energy investment in growth should be placed where the average irradiance is highest and the payback is therefore highest". They used LMA as the index of biochemical capacity for CO_2 assimilation. Their model was also based on the three-parameter equation of Johnson and Thornley (1984). But light-saturated photosynthetic rate and half-saturated irradiance can be monotonic increasing functions or saturating functions of LMA. As a result, the optimal profile of LMA is broadly comparable with those seen in their field data.

Evaluating optimality

We now compare, as suggested by the previous optimization theories, the observed rate constants for LMA (or for area-based nitrogen content) with the extinction of the radiation-weighted time-mean photosynthetic photon flux density $\bar{k}$. It may be written as (see details in Sellers et al, 1992):

$$\bar{k} = \int\int_{\text{time}} [G(\mu)/\mu]\,(1-\omega_V)^{1/2}\,dt\,d\tau \qquad [6]$$

where ω_V is the leaf scattering coefficient in the PPFD domain, and is equal to transmittance plus reflectance (see Major et al, 1993), $G(\mu)$ is the relative projected area of leaves in direction $\cos^{-1}\mu$ and μ is the cosine of the solar zenith angle. This simplest model assumes that the sun is a point-source, foliage is distributed randomly in space and the leaf inclination is invariant with height. Leaf growth-irradiance history must be considered by integrating over both day-length and expansion periods. As an example, we chose to calculate $\bar{k}$ for two locations near Montpellier in southern France (latitude 43°36'N), Camp-Redon and Puechabon (see table II). Leaf expansion of *Q ilex* began on approximately Julian day 100 and ended on Julian day 180 (Damesin, unpublished data). Measurement of ω_V for this species gave about 12% (ie, reflectance = 10.7% and transmittance = 1.4%). We assumed here, as Hollinger (1984) did for *Q agrifolia*, the inclination angles of leaves distributed uniformly over the surface of a sphere, that is a spherical Poisson model. In this case, G takes a value of 0.5 for all solar elevation angles. The corresponding $\bar{k}$ is 0.72, an extinction coefficient far higher than the rate constants observed for the LMA (range 0.088–0.294) and for the area-based nitrogen or total structural content in both *Q ilex* and *Q coccifera* canopies even in their driest locations. Measurements and simulations done by Caldwell et al (1986) on nine *Q coccifera* canopies of LAI ranging from 2.1 and 8.2 validate our estimate of $\bar{k}$.

Consequently, the relative cumulative PPFD reaching leaves that grow at the bottom of the canopy considered were only 5 and 12% of the full sun for Camp-Redon and Puechabon, respectively. Inferred from carbon isotope composition, the ratio of water-use efficiencies for upper and lower leaves that we assumed to experience the same leaf-to-air vapor pressure gradient Δw were 44 and 49% for Camp-Redon in 1990 and 1993, and 59% for Puechabon in 1993 (see eq 2 and table III). These last results suggested that Mediterranean evergreen oak canopies are in some way optimal or 'nearly' optimal. However, the optimal vertical pattern of leaf parameters for carbon gain depends on numerous factors, only some of which are discussed in this paper. Our results tend to partly confirm the underlying assumptions of Field (1983), Hirose and Werger (1987) and Chen et al (1993), who assumed that profiles of leaf physiological properties within the canopy follows the radiation-weighted time-mean profile of PPFD and that leaf nitrogen is continuously partitioned or 'coordinated' in such a way as to maintain a balance between the rubisco-limited rate of carboxylation and the electron transport-limited rate of carboxylation. However, if Meister et al (1987) concluded that measured distribution of leaf photosynthetic properties within *Q coccifera* canopies was 'nearly optimal', further studies will be necessary to interpret site differences in the LMA profiles and to find on what principle can this control be based.

CONCLUSION

Leaf mass per area also known as specific leaf weight or specific leaf mass is an important link between plant carbon and water budgets because it describes the distribution of plant biomass relative to leaf area within a canopy. Mediterranean evergreen oak species acclimate to increased light availability within the canopy by producing a gradient of leaves that are morphologically as well as physiologically distinct. LMA is particularly sensitive to increased light availability and tends to follow time-averaged irradiance levels. LMA varies with site water availability and leaf parameters were related to the difference in LMA within and between sites. Changes in LMA are accompanied by changes in the photosynthetic apparatus per unit leaf area and hence changes in area-based photosynthetic capacity. Differences in photosynthetic capacity of leaves exposed to different levels of PPFD may arise from variation in both LMA and differential allocation to photosynthetic enzymes vs light-harvesting machinery, both of which contribute to variation in area-based nitrogen content and to 'nearly' maximize whole-carbon gain. Our results suggest that a morphological index, LMA, could by itself possibly be used as a criterion indicating normal physiological activity and may contribute significantly to a broader application of photosynthesis models at the community and landscape levels (Pierce et al, 1994).

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