Leaf mass per area ratio in *Quercus ilex* leaves under a wide range of climatic conditions. The importance of low temperatures

Romà Ogaya*, Josep Peñuelas

Unitat d'Ecofisiologia CSIC-CEAB-CREAF, CREAF (Centre de Recerca Ecològica i Aplicacions Forestals), Universitat Autònoma de Barcelona, E-08193 Bellaterra, Barcelona, Spain

**Abstract**

The Digital Climatic Atlas and the Ecological and the Forestry Inventory of Catalonia (NE Spain) were analysed to study the climate effect on leaf mass per area (LMA) and leaf area index (LAI) on *Quercus ilex* L., one of the most widely spread tree species in the Mediterranean region. 195 sites in this region of 31,895 km² were considered. The relationship between climatic variables (total annual rainfall, mean annual temperature, mean minimum winter temperatures, and mean annual solar radiation) and LMA and LAI were analysed by simple and multiple regressions. LMA was higher in the drier sites and specially in the colder sites. There was also a significant correlation between solar radiation and LMA. On the contrary, LAI values, which were negatively correlated with LMA values, were lower in drier and colder sites, and were not significantly affected by solar radiation. The results highlight that high LMA values do not seem to be a specific protection to dry conditions but to a wide range of environmental stress factors, including low temperatures.

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1. Introduction

Climate influence on leaf traits such as morphology, longevity, nutrient content, and photosynthetic rate are widely described in all biomes of the world (Field and Mooney, 1986; Reich et al., 1992, 1997; Niinemets, 2001; Wright et al., 2004; Traiser et al., 2005). A large number of studies have related high LMA with evergreeness, long leaf longevity, thick cuticle, low nitrogen content, and low photosynthetic rates (Körner, 1989; Turner, 1994; Eamus and Prichard, 1998; Aerts, 1995; Yin, 2002). They are related with high solar irradiance (Chabot and Chabot, 1977; Sobrado and Medina, 1980; Yun and Taylor, 1986; Witkowski and Lamont, 1991; Groom and Lamont, 1997), and drought conditions (Salleo and Lo Gullo, 1990; Witkowski and Lamont, 1991; Turner, 1994; Groom and Lamont, 1997; Niinemets, 2001).

Mediterranean environments are characterized by summer drought as the most critical period for plant development (Mooney, 1983) but winter cold is also described as an important factor limiting plant photosynthetic rate and growth (Mitrakos, 1980; Terradas and Savé, 1992; Larcher, 2000; Oliveira and Peñuelas, 2000, 2001, 2002, 2004). Holm oak (*Quercus ilex* L.) is a drought-adapted tree widely distributed in the Mediterranean Basin (Fig. 1; Debazach, 1983; Terradas, 1999), but this species...
show lower resistance to dry conditions and higher tolerance to low temperatures than other co-occurring Mediterranean trees or shrubs such as Phillyrea latifolia (Lloret and Siscart, 1995; Peñuelas et al., 1998, 2000; Ogaya and Peñuelas, 2003), so Q. ilex must compete with more drought-tolerant species in the driest sites of its distribution and with temperate species in the more mesic environments, where winter cold poses severe limitations on Q. ilex photosynthetic activity and growth (Oliveira and Peñuelas, 2000, 2001; Tretiach, 1993; Tretiach et al., 1997).

In Q. ilex, low LMA values during the wettest periods have often been observed (Gratani, 1996; Gratani and Varone, 2006), and LMA values were lower in leaves of resprouts than in leaves of undisturbed trees in a clear-cut experiment (Peña-Rojas et al., 2005). On the other hand, winter cold increases leaf photoinhibition and LMA values in response to cold temperatures (Oliveira and Peñuelas, 2004). Moreover, Clemente et al. (2005) have observed lower LMA in seedlings and resprouts than in mature Mediterranean plants before a fire due to lower water availability for seedlings and resprouts.

We aimed to study the influence of the different climatic variables (temperature, radiation, and rainfall) on LMA, LAI and foliar nitrogen concentrations of Q. ilex trees living in the field under a wide range of climatic conditions. Our focus was to discern the effect of other environmental stressors apart from the well known drought effects.

2. Materials and methods

The data of this work were obtained from the Ecological and Forestry Inventory of Catalonia (CREAF, Barcelona, 2003) [http://www.creaf.uab.es/iefc/] and from the digital climatic atlas of Catalonia [http://magno.uab.es/atles-climatic/] (Pons, 1996; Ninyerola et al., 2000). One hundred well-developed mature leaves from several Quercus ilex mature trees were randomly collected from different parts of the canopy, and they were used to measure LMA in each one of 195 plots of this forestry inventory (Fig. 1). The 195 plots were monitored (one time per plot) in campaigns throughout the whole year and only well-developed mature leaves were collected. Nearby plots in space (but with different climatic conditions due to local orography) were measured during the same period, and some plots with similar climate but well separated in space from each other were measured during different periods within the year. Therefore there were clusters of plots with similar climate measured at different times of the year, greatly buffering the variance associated to the measurement period. Each one of the 19,500 leaves (each sample was obtained with a hole punch) were weighted after drying at 70°C in an oven during three days, and LMA values were calculated by the ratio of leaf dry weight and the leaf surface area of the hole punch. The arithmetic mean values of LMA of the 100 single leaf samples per plot were used for stand level analyses. In 53 plots, all leaves sampled at a plot were combined to a bulk sample; this bulk was crushed and dried (75°C), and foliar nitrogen concentration in each one of those 53 plots was measured using an elemental analyser (Model NA 1500, Carlo Elba Instrumentazione, Milan, Italy). LAI was obtained from allometric relationships between stem diameter and tree leaf biomass calculated for each one of the 195 sites (always highly significant, p < 0.001).

Total annual rainfall, mean annual solar radiation, and mean annual and mean minimum winter temperatures (obtained from meteorological stations data, from 1951 to 1999) were depicted in each one of the considered plots inserting plot coordinates in the digital climatic atlas. In the atlas, climatic data were interpolated for each point in the map (360 m between two consecutive points) with regressions between climatic variables and geographical variables, and the regressions were readjusted with climatic data obtained.
from the meteorological stations (see detailed descriptions in http://magno.uab.es/atles-climatic/; Pons, 1996; Ninyerola et al., 2000).

2.1. Statistical analyses

Simple linear regressions were conducted to examine the relationships between LMA values and total annual rainfall ($P$), mean annual solar radiation ($R$), mean annual temperature ($T_{\text{mean}}$), and mean minimum winter temperatures ($T_{\text{min}}$). Two multiple linear regressions were conducted to test meteorological influence on LMA values, the first multiple regression was conducted with LMA values as dependent variable and total annual rainfall, mean annual solar radiation, and mean annual temperature as predictor variables, and the other multiple regression was conducted with LMA values as dependent variable and total annual rainfall, mean annual solar radiation, and mean minimum winter temperatures as predictor variables. In these two multiple regressions, the forward stepwise regression technique was used.

Other simple linear regressions were conducted to examine the relationships between LMA and LAI values, and between LMA and foliar nitrogen concentration values. Other multiple linear regressions analyses were conducted to test climatic relationships with LAI and foliar nitrogen concentration values. All regressions were performed with the Statistica software package (Statsoft Inc., Tulsa, OK, USA).

3. Results

At the regional scale of this study, the range of climatic conditions of the studied Catalonia Q. ilex forests is very large including most of the typical climatic environments of the Mediterranean region. The annual rainfall ranged from 436 to 1157 mm, the mean annual solar radiation from 10.9 to 17.1 MJ m$^{-2}$ day$^{-1}$, the mean annual temperature from 7.4 to 15.4 °C (Fig. 2), and the mean minimum winter temperature from −4.4 to 5.2 °C.

LMA was negatively related to total annual rainfall, mean annual temperature, and mean minimum winter temperatures, and it was positively correlated with solar radiation (Fig. 3). The relationship between LMA and rainfall was very weak ($R^2 = 0.03; P = 0.014$). It was slightly stronger with solar radiation ($R^2 = 0.16; P < 0.001$). The strongest climatic relationship was that with air temperatures ($R^2 = 0.26$ and $R^2 = 0.34$ for

Fig. 2 – Total annual rainfall (a); mean annual air temperature (b); and solar radiation (c) of Catalonia (from the digital climatic atlas of Catalonia) (Ninyerola et al., 2000; Pons, 1996). The location of the studied sites are depicted with asterisks.

Fig. 3 – Linear relationships between LMA (leaf per mass area) values of Q. ilex in the 195 studied sites of Catalonia and total annual rainfall (a); solar radiation (b); mean annual air temperature (c); and mean minimum winter air temperatures (d).
mean annual temperature and mean minimum winter temperatures, respectively; and $P < 0.001$ in both cases; Fig. 3). LMA was logarithmically and negatively correlated with LAI ($R^2 = 0.38; P < 0.001$), and LMA was negatively correlated with foliar nitrogen concentrations ($R^2 = 0.14; P = 0.006$, Fig. 4).

Stepwise multiple regressions showed a strong influence of precipitation, temperature and radiation on LMA values ($R^2 = 0.42$ or $R^2 = 0.45$ depending on whether mean annual temperature or mean minimum winter temperatures are considered; $P < 0.01$ in both cases) (Table 1). LAI values were also dependent on climatic conditions, but less than LMA values ($R^2 = 0.25$ and $R^2 = 0.30$ when mean annual temperature and mean minimum winter temperatures were considered, respectively; $P < 0.001$ in both cases; Table 1). LAI was positively correlated with total annual rainfall, mean annual temperature, and mean minimum winter temperatures, and was slightly negatively correlated with solar radiation: $\text{LAI} = 1.24 + 0.004 \text{P}$, $R^2 = 0.12$; $P < 0.001$, $\text{LAI} = 0.44 + 0.18 \text{Tmean}; R^2 = 0.04$; $P = 0.003$, $\text{LAI} = 1.67 + 0.23 \text{Tmin}; R^2 = 0.11$; $P < 0.001$, and $\text{LAI} = 4.81 - 0.002 \text{R}; R^2 = 0.03; P = 0.012$. Foliar nitrogen concentrations were not significantly correlated with any climatic variable.

### Table 1 – Multiple linear regression equations for LMA (leaf per mass area) and LAI (leaf area index) values for Q. ilex depending on different climatic variables: “P” is total annual rainfall (mm), “Tmean” is mean annual temperature ($^\circ$C), “Tmin” is mean minimum winter temperatures ($^\circ$C), and “R” is solar radiation (MJ m$^{-2}$ day$^{-1}$)

<table>
<thead>
<tr>
<th>Equation</th>
<th>$R^2$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\text{LMA} = 37.24 - 0.011 \text{P} - 1.399 \text{Tmin} + 0.004 \text{R}$</td>
<td>0.45</td>
<td>$&lt; 0.001$</td>
</tr>
<tr>
<td>$\text{LMA} = 38.79 - 0.012 \text{P} - 0.141 \text{Tmean} + 0.004 \text{R}$</td>
<td>0.42</td>
<td>$&lt; 0.001$</td>
</tr>
<tr>
<td>$\text{LAI} = 2.25 + 0.005 \text{P} + 0.306 \text{Tmin}$</td>
<td>0.30</td>
<td>$&lt; 0.001$</td>
</tr>
<tr>
<td>$\text{LAI} = -6.66 + 0.005 \text{P} + 0.343 \text{Tmean}$</td>
<td>0.25</td>
<td>$&lt; 0.001$</td>
</tr>
</tbody>
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4. Discussion

The results showed negative correlation between LMA and temperature i.e. they did not apparently fit with those of a recent comprehensive study that considered a great amount of vascular plant species (2370) from a wide range of vegetation types around the world (163 sites), in which in general a low climate influence on leaf traits was found, but in which LMA values increased when temperature increased (Wright et al., 2004). As expected, in our study LAI values were lower in driest sites, showing lower transpirational surface, but LAI values increased also with temperature, despite of the high evaporative demand of the warmest sites. The relationship between LAI and temperature could indirectly explain a part of the inverse relationship between LMA and LAI, because lower LAI values were found at colder sites and LMA was inversely correlated with temperature. But the major part of the inverse relationship between LMA and LAI must be accounted for a LAI effect by itself because the relationship between LAI and temperature was very weak. LAI values can vary in the same site depending on the local topography (i.e. the top of a ridge, the bottom of a valley...) (Sala et al., 1994).

Canopies with low LAI values have a greater proportion of sun leaves than canopies with high LAI values, and sun leaves have larger LMA values than shade leaves (Sala et al., 1994).

The unexpected low LMA and high LAI values with high temperatures, and the inverse relationship between LMA and LAI suggest that under higher water availabilities and warmer temperatures, Q. ilex tends to have more leaves with less LMA, which is more efficient to maximize photosynthetic gain. But under harsher climatic conditions such as lower water availabilities and lower temperatures, Q. ilex plants invest more resources in strong and rigid leaves to resist climatic adversities. High LMA values in Mediterranean vegetation are often related to leaf resistance to dry conditions (Harley et al., 1987; Kyparissis and Manetas, 1993; Gratani, 1996; Niinemets, 2001), and to high vapour pressure deficit and potential evapotranspiration (Wright et al., 2004). The results of this study show higher LMA values in Q. ilex leaves in conditions of low air temperatures, despite of relative high water availability of cold sites compared to hot sites. Winter cold poses strong limitations to the photosynthetic activity in Mediterranean plants, and leaves with higher LMA seem to be more capable to resist low temperatures (Oliveira and Peñuelas, 2002, 2004). In Q. ilex seedlings, lower leaf area is observed in plants from...
colder sites and higher leaf density in plants from hotter sites, which provides higher photosynthetic rates for smaller leaves at low temperatures and higher water use efficiency for more dense leaves at high temperatures (Gratani et al., 2003). A recent study conducted with different European flora species also revealed minimum temperatures were the most important factor influencing some physiognomic characters such as leaf size, which is lower in colder sites (Traiser et al., 2005).

In this Mediterranean species, Q. ilex, high LMA values did not seem to be a protection only against dry conditions, indicating that a high LMA is a good adaptation trait to a wide range of environmental stresses and not exclusive to any particular one (Turner, 1994).

Acknowledgments

We are grateful to Teresa Mata and Joan Josep Ibáñez for supplying the data from Inventari Ecològic i Forestal de Catalunya. This research was financially supported by MEC projects REM2003-04871, and CGL2004-01402/BOS from the Spanish Government, by the European project ALARM (Contract 506675, EU sixth framework programme) and by a Fundació BBVA 2004 and a SGR2005-00312 AGAUR-Generalitat de Catalunya grants.

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