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Original article

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

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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 km^2 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.

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; Witkowsky and Lamont, 1991; Groom and Lamont, 1997), and drought conditions (Salleo and Lo Gullo, 1990; Witkowsky 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

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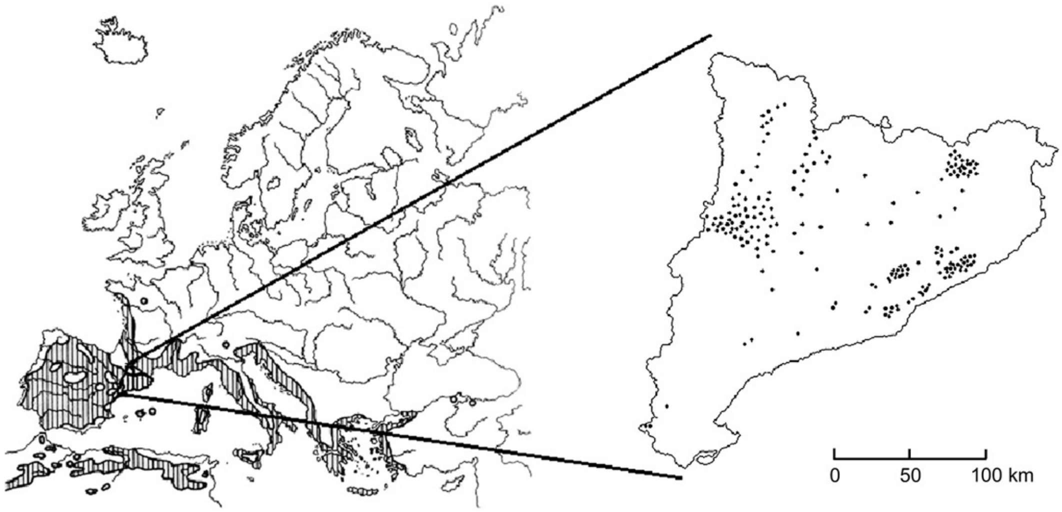

Fig. 1 – *Quercus ilex* L. distribution in the Mediterranean basin and localization of the 150 sites from the Ecological and Forestry Inventory of Catalonia where we sampled *Q. ilex* leaves.

shows 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 higher 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