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Review

Photosynthetic limitations in Mediterranean plants: A review

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ABSTRACT

The aim of the present work is to review the literature concerning photosynthesis of Mediterranean plants. First, we briefly review the most important environmental constraints to photosynthesis, i.e. chilling winter temperatures and summer drought. Then, the review specifically focus on the photosynthetic capacity and photosynthetic limitations of Mediterranean plants under non-stress conditions, to test the general assumption that that the photosynthetic capacity of Mediterranean plants is lower than that of plants from other biomes. It is shown that Mediterranean plants of different life forms and leaf types present, on average, similar photosynthetic capacity to plants from any other biome. However, the mechanisms potentially limiting maximum photosynthesis differ between Mediterranean and non-Mediterranean species. For instance, Mediterranean plants compensate their lower mesophyll conductance to CO_2 (g_m) with a larger velocity of carboxylation ($V_{c,max}$) to achieve similar photosynthesis rates (A_N) to non-Mediterranean plants, both factors being associated to a larger leaf mass area (LMA) in Mediterranean species. In contrast, stomatal conductance (g_s) was found to be lower only in Mediterranean sclerophytes. On the other hand, Mediterranean sclerophytes and malacophytes (but not herbs and mesophytes) show higher mean intrinsic water use efficiency (A_N/g_s) due to a combination of higher g_m/g_s and A_N per unit CO_2 concentration in the chloroplasts, i.e. carboxylation efficiency.

The described variations in the mechanistic components of photosynthesis may represent specific adaptations of Mediterranean plants to their environment, leading these plants to achieve high A_N despite their large LMA, and Mediterranean ecosystems to be among those presenting the largest net primary productivities worldwide.

Contents

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1. Introduction

The landscape of Mediterranean-type ecosystems is dominated by evergreen sclerophyll forests, woodlands of either evergreen sclerophylls or semideciduous malacophylls, and grasslands. Although diverse and variable, these ecosystems present lower standing biomass per hectare than non-Mediterranean ecosystems, such as tropical broadleaf evergreen forests and temperate deciduous forests (Potter, 1999). Woody evergreen sclerophyll plants, that exhibit low specific leaf area, are indeed slow-growing species (Reich et al., 1992; Galmés et al., 2005). This, coupled with cold winters and hot/dry summers typical of Mediterranean climate, which restrict the favorable periods for photosynthesis to a few weeks in spring and autumn, originated the assumption that the photosynthetic capacity of Mediterranean plants (Folch and Camarasa, 1999) and the productivity of Mediterranean ecosystem were quite low (Ehleringer and Mooney, 1983). It is noted that most reviews on photosynthetic performance of Mediterranean plants, as well as the techniques adopted for estimating gas exchange, are outdated (Margaris, 1981; Ehleringer and Mooney, 1983; Ne′eman and Goubitz, 2000). The increasing popularity of portable infra-red gas analysers in the 90s, and the introduction of eddy-flux technique for direct assessment of gas exchange and productivity at the canopy level have allowed the accumulation of a larger amount of data. Therefore, a more precise picture of the photosynthetic limitations in Mediterranean plants can now be drawn. Moreover, the combination of gas exchange and chlorophyll fluorescence measurements in addition to carbon isotope discrimination allows estimations not only of the net CO_2 assimilation rate and stomatal conductance, but also of the mesophyll conductance to CO_2 and the rate of gross photosynthesis. Altogether it is now possible to address the mechanisms that limit photosynthesis in Mediterranean plants (Grassi and Magnani, 2005).

A review of the literature concerning photosynthesis in Mediterranean plants is presented. First, the most important environmental constraints to photosynthesis, i.e. chilling winter temperatures (T) and summer drought are reviewed. Then, three main questions of plants under non-stressed conditions are addressed: (1) is the photosynthetic capacity of Mediterranean plants lower than plants of other biomes? (2) What about the intrinsic photosynthetic water use efficiency of Mediterranean plants? (3) Do Mediterranean plants differ from plants in other biomes for traits that favor photosynthesis, such as stomatal (g_s) and mesophyll (g_m) conductances to CO_2 and the maximum carboxylation velocity ($V_{c,max}$)? Finally, there is a brief discussion about the photosynthetic capacities and limitations of typical Mediterranean crops.

1.1. *Environmental constraints to photosynthesis under Mediterranean conditions*

Based on annual trends of photosynthesis estimated at mid-morning, it appears evident that maximum rates occur in spring and autumn, whereas depressions in photosynthesis of variable magnitude are detected in winter and summer (Eckardt et al., 1977; Tenhunen et al., 1987; Tretiach, 1993; Castell et al., 1994; Damesin and Rambal, 1995; Gratani, 1995; García-Plazaola et al., 1997; Peñuelas and Llusía, 1999; Haase et al., 2000; Méthy et al., 2000; Flexas et al., 2001; Ogaya and Peñuelas, 2003; Gratani and Varone, 2004; Gulías et al., 2009). Therefore, chilling temperatures during winter and hot/dry summer (i.e. drought) are the most limiting factors for photosynthesis under Mediterranean conditions. Indeed, the distribution of Mediterranean species along a latitudinal gradient depends on the species-specific adaptation to these environmental constrains (Mitrakos, 1980). The extent to which the photosynthesis rate of an individual species is depressed in winter/summer may depend on both species-specific adaptations and

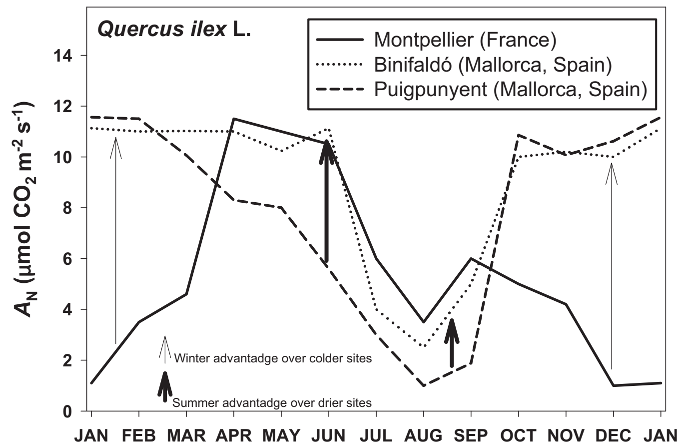

Fig. 1. Annual variations of photosynthesis of the evergreen sclerophyll tree *Quercus ilex* (holm oak) at three different locations: Montpellier (data from Méthy et al., 2000), Binifaldó and Puigpunyent (data from Gulías et al., 2009). Thin arrows indicate the photosynthetic advantage of plants growing at Binifaldó over those growing at the colder site Montpellier during winter, while thick arrows indicate the photosynthetic advantage of plants growing at Binifaldó over those growing at the drier site Puigpunyent during summer. Modified after Flexas et al. (2003).

climatic conditions of individual Mediterranean sites. This is presented in Fig. 1 by comparing published data of annual trends of daily photosynthesis rates in *Quercus ilex* growing at three different locations: Montpellier (South of France, average year precipitation –AYP– of 750 mm, and minimum monthly temperature –MMT– of 1 °C), Binifaldó (Mallorca, Spain, AYP 1050 mm, MMT 8 °C), and Puigpunyent (Mallorca, Spain, AYP 450 mm, MMT 12 °C). Minimum photosynthesis was observed in winter at the coldest site (Montpellier) and in summer at the hottest and driest site (Puigpunyent). Photosynthesis was much higher in Binifaldó than at Montpellier during winter periods (indicated by thin arrows), and substantially higher than in Puigpunyent during summer (indicated by thick arrows), which is characterized by mild temperatures and relatively high yearly precipitation. Year-round maximum net photosynthesis averaged 5.5, 9.5 and 8.0 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ at Montpellier, Binifaldó, and Puigpunyent, respectively. Using these rates as rough proxies of year carbon balance (at the leaf level) and following Mitrakos (1980), *Q. ilex* should be preferentially distributed at Binifaldó, where it indeed dominates the arboreal ecosystem coverage, and less at cooler sites like Montpellier (where it is indeed less dominant in mixed stands with deciduous *Quercus* species) and at the drier site like Puigpunyement (where there are indeed only few trees within a shrub *macchia* stand). Similar findings have been reported by Corcuera et al. (2005) who concluded that *Q. ilex* is more sensitive to winter than to summer stress.

Besides different *magnitudes* in the depression of photosynthesis during winter or summer the *mechanistic causes* for such depressions may differ between winter and summer and will be discussed in the next sections. It is out of the aim of this review to elucidate the responses of photosynthesis in Mediterranean plants to other stresses such as nutrient availability (Daas-Ghrib et al., 2011), ozone (Mereu et al., 2011; Velikova et al., 2005; Lombardozzi et al., 2012), UV-radiation (Llusía et al., 2012) or excess soil salinity (Redondo-Gomez et al., 2008).

1.2. *Photosynthesis limitations in winter*

Based on response curves of photosynthesis to air T under controlled conditions, most Mediterranean plants show an optimum T for photosynthesis in the range 15–30 °C, the most common being 25–30 °C (Oechel et al., 1980; Larcher, 2000; Ogaya and Peñuelas, 2003). However, under Mediterranean field conditions low T are