



Photosynthetic responses to stress in Mediterranean evergreens: Mechanisms and models



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ABSTRACT

Plants in Mediterranean ecosystems face multiple environmental stresses during the growing season. Such stresses greatly affect ecosystem function, but are poorly represented by current ecosystem models. Here, we review recent advances in understanding the responses of ecosystem photosynthesis to drought and photoinhibition. Reductions in canopy net assimilation rates by recurrent water limitations during the day and during drought periods result from multiple limitations at the biochemical, cellular and structural levels, including reductions in stomatal, and mesophyll diffusion conductances, foliage biochemical potentials, light harvesting efficiency and modifications in canopy structure. Overall, a hierarchy of environmental effects, from instantaneous, short- and long-term influences, shape photosynthetic responses to stress in the field. The processes involved can be incorporated into photosynthesis models to different degrees, given our current understanding of each. However, fully mechanistic consideration of certain phenomena such as non-reversible, hysteretic and lagged heat and drought effects, or photoinhibition, would require the use of models including dynamic damage and repair mechanisms. We outline further model and experimental work needed to describe the parameter space for quantitative simulation of such phenomena, especially considering the need to simulate plant production under global change.

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1. Introduction

1.1. Stress in Mediterranean ecosystems

The Mediterranean climate is characterized by hot and dry summers, leading to a seasonally recurring drought stress (Allen, 2001; Lionello et al., 2006) that strongly limits plant photosynthetic productivity (Beyschlag et al., 1987b; Chaves et al., 2002; Flexas and Medrano, 2002a; Pereira et al., 2007; Rambal et al., 2003; Reichstein et al., 2002, 2003; Tenhunen et al., 1987a). Indeed, water availability is known to be the main limiting factor to plant photosynthesis globally (Boyer, 1982; Nemani et al., 2003). Mediterranean ecosystems have therefore adapted to deal with prolonged periods of water shortage, though a wholly mechanistic understanding of the interplay of diverse plant strategies to deal with water stress is still lacking (e.g., Flexas and Medrano, 2002a; Gulías et al., 2009; Lawlor and Tezara, 2009; Loreto and Centritto, 2008). Climate change projections suggest that higher temperatures, as well as changes in seasonal precipitation patterns (Meehl et al., 2007), will aggravate the seasonal drought stress characteristic to Mediterranean

ecosystems (Beniston et al., 2007; Christensen et al., 2007; Giorgi, 2006; Giorgi et al., 2004). Although annual precipitation itself may increase in some regions such as northern Europe and northern part of North America, much of this increase is predicted to be associated with enhanced winter precipitation (Christensen et al., 2007). Thus, as a whole, the importance of drought is expected to increase worldwide (e.g., Schwalm et al., 2012). It is therefore imperative to develop a robust understanding of the mechanisms plants use to cope with drought stress, and Mediterranean ecosystems provide an excellent test-bed to analyze drought response mechanisms.

While drought can be considered as a key limitation in Mediterranean climates, the environmental setup is much more complex. In open sites and at the top of plant canopies, drought often interacts with high temperatures, and high quantum flux densities, especially under conditions of reduced convective cooling in leaves with closed stomata (Niinemets, 2010b; Valladares and Pearcy, 1997), potentially resulting in heat stress and photoinhibition. In contrast, plants in understory and in low canopy may have reduced photosynthesis due to low light availability (Eckardt et al., 1977; Meister et al., 1987; Niinemets et al., 2006a; Tenhunen et al., 1987b; Valladares and Guzmán, 2006; Wagner et al., 1993). Despite severe water limitations, many Mediterranean communities may support relatively high leaf area indices such that light levels in the understory can often decrease to only 5–15% of above-canopy

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light (Niinemets et al., 2006a; Puértolas et al., 2010; Valladares and Guzmán, 2006). On the other hand, shallow-rooted seedlings may suffer from more severe drought stress in shade than open-grown plants and larger plants (Aranda et al., 2005; Valladares and Percy, 2002; Valladares et al., 2008). Plants gradually recover from drought in autumn and winter, but the physiological activity can be strongly curbed by low temperatures, occasionally by frost stress (Gimeno et al., 2009, 2012; Martínez-Ferri et al., 2004) that together with high light intensities can lead to severe downregulation of photosynthetic activity (Camarero et al., 2012; Corcuera et al., 2005).

1.2. Physiological and structural responses to stress: common vs. contrasting mechanisms

Due to the seasonally recurring drought stress, plants in Mediterranean ecosystems have developed a variety of physiological and structural mechanisms to help them survive episodic water limitations and co-occurring other stresses. At the leaf scale, stomatal, mesophyll and biochemical responses together with structural adaptations to drought stress interact to improve the plant ability to survive drought. At the leaf scale, stomata are the primary regulators of leaf hydrology, and represent an important means by which plants regulate water use in response to stress. Classical studies have demonstrated that stomatal closure in response to drought stress in Mediterranean ecosystems is typically correlated with lower transpiration rates and an increase of resistance to CO₂ diffusion in leaves (Kaiser, 1987; Tenhunen et al., 1984b, 1987a). Whether or not stomatal closure is the primary response of the photosynthetic apparatus to drought is highly debated (e.g., Flexas et al., 2012; Flexas and Medrano, 2002a; Tenhunen et al., 1984a). Conflicting reports in the literature show that the effects of water stress on photosynthesis can be either dependent (e.g., Dietz and Heber, 1983; Schwab et al., 1989) or independent (e.g., Cornic et al., 1989; Kaiser, 1987) of stomata or the controls can be shared by stomatal and non-stomatal factors (Flexas and Medrano, 2002a for a review). Nevertheless, the majority of the studies does demonstrate a reduction of CO₂ concentration in sub-stomatal cavities under drought stress (Flexas et al., 2001; Flexas and Medrano, 2002a; Grassi and Magnani, 2005; Mediavilla and Escudero, 2003; Medrano et al., 2002; Tenhunen et al., 1981, 1985; Xu and Baldocchi, 2003), indicating that stomatal closure to conserve water does generally play an important role in reductions in photosynthesis.

In addition to diffusive limitations by stomata, the concentration of CO₂ at the site of its fixation in the chloroplasts is dependent on resistances inside the leaf mesophyll (Flexas et al., 2008, 2012; Loreto et al., 1992), and some studies have demonstrated enhanced diffusive limitations from sub-stomatal cavities to chloroplasts (reduced mesophyll diffusion conductance) in water-stressed leaves (e.g., Cornic and Massacci, 2004; Loreto et al., 1992, 2003) and an impairment of the biochemical and photochemical reactions in response to water stress (e.g., Tang et al., 2002; Tezara et al., 1999). In particular, impaired Rubisco activity and its substrate ribulose-1,5-bisphosphate (RuBP) regeneration, impaired photophosphorylation and photoinhibition have been reported (Flexas and Medrano, 2002b), with the inactivation of Rubisco being suggested to be the main response of photosynthesis to drought (Arend et al., 2013; Parry et al., 2002; Tezara et al., 1999). Characterizing the nature of these responses under different levels of drought stress is essential to enable the development of accurate models.

The rich variety of responses has led to a series of studies examining whether stomatal, mesophyll or biochemical limitations are the main cause for decreased photosynthesis under water stress (Egea et al., 2011; Grassi and Magnani, 2005; Keenan and Gracia, 2010a). In particular, application of the quantitative

limitation analysis has shown some success at disentangling the relative contributions of different mechanisms to the response of photosynthesis to drought stress. First proposed by Jones (1985), the approach makes it possible to calculate relative limitations to assimilation over any period of time, assuming that a reference maximum assimilation rate can be defined as a standard. Grassi and Magnani (2005) extended the technique to partition the photosynthetic response between stomatal, mesophyll and biochemical limitations, and it has been demonstrated that all three limitations do significantly curb plant photosynthesis rate (Flexas et al., 2012; Grassi and Magnani, 2005; Tomás et al., 2013).

In addition to the leaf-level responses, multiple strategies exist that modify canopy structural properties in response to drought stress. These include changes in total canopy leaf area, the aggregate leaf inclination angle, leaf age composition and leaf clumping (Niinemets and Anten, 2009; Percy et al., 2005; Valladares and Niinemets, 2007; Valladares and Percy, 1997). Each of these traits can serve to alter distribution of radiation through the canopy, and thus, modify environmental conditions and severity of stress at different canopy layers, thereby altering whole canopy photosynthesis (Niinemets and Anten, 2009). Furthermore, redistribution of available resources to more efficient leaves adapted to high irradiances in the canopy and modification of distribution of hydraulic conductances can also importantly alter whole plant photosynthesis and water use (Niinemets, 2012; Peltoniemi et al., 2012). None of these mechanisms are routinely included in land surface models, although the effects can be very important in Mediterranean species (Caldwell et al., 1986; Sala and Tenhunen, 1996; Tenhunen et al., 1990). This poor consideration of multiple important adaptive modifications is due both to the lack of observations available for model parameterization, and the lack of a consensus as to what are the primary responses to drought stress.

The wide variety of observed mechanisms and limited information on the relative role of each individual adaptive response (e.g., Grassi and Magnani, 2005; Keenan and Gracia, 2010a) makes modeling Mediterranean ecosystems challenging (Vargas et al., 2013). Furthermore, there is limited information on how different responses vary temporally, spatially, and both between and within species. Here, we set out the current state-of-the-science of mechanistic responses of Mediterranean forest canopy photosynthesis to environmental stress, both in terms of our theoretical understanding and our ability to model them at the leaf and canopy scales. Photosynthesis under Mediterranean conditions has been recently thoroughly reviewed by several papers (Chaves et al., 2009; Flexas et al., 2009; Galmés et al., 2012). Here we consider a series of representative case studies of stress-dependent variations in foliage photosynthetic characteristics and refer to these excellent reviews for the in-depth coverage of variability of photosynthetic responses to stress under Mediterranean conditions. We start with outlining the characteristic variation patterns of photosynthesis in Mediterranean conditions, then set up the basic modeling framework to consider drought, photoinhibition and high temperatures on photosynthesis, describe distribution of various physiological limitations under stress, analyze the role of canopy processes and finally propose a general framework to simulate plant photosynthesis in Mediterranean ecosystems.

2. Stress-dependent variations in foliage photosynthetic characteristics in Mediterranean ecosystems

2.1. Diurnal variations under well-watered and water-stressed conditions

The Mediterranean growing season is typically associated with high temperatures, high quantum flux densities (Fig. 1a) and high

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