Journal of Arid Environments xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Leaf thickness and density drive the responsiveness of photosynthesis to air temperature in Mediterranean species according to their leaf habitus

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ARTICLE INFO

Keywords:
Multi-year dataset
Evergreen
Leaf morphology
Leaf trait co-variations
Standardized major axis regression

ABSTRACT

The responsiveness of net photosynthetic rate (A_a) to mean monthly air temperature (T_M) of eight Mediterranean evergreen species was investigated by analyzing the inter-annual changes in leaf mass area (LMA), leaf tissue density (LTD) and leaf thickness (LT). We wanted to test if species leaf habitus affected this response. To hit the goal, a multi-year dataset from our previously published papers was used. The inter-annual variability in LMA, LTD and LT was assessed by their coefficients of variation (CVs). A_a sensitivity to T_M (SA_a) was quantified by the slope of the species-specific relationships A_a-T_M. A Principal Component Analysis (PC) was carried to identify the leaf morphological variation patterns across species. SA_a was affected by the coordination of LTD and LT across species and this coordination depended on leaf habitus. The relationship between CVs and SA_a revealed that only evergreen sclerophyllous with a longer leaf life-span rely on the inter-annual changes in LTD and LT to modulate their SA_a. Overall, the results showed that the inter-annual LTD and LT variability affected the responsiveness of net photosynthetic rate of the selected species according to their leaf habitus.

1. Introduction

Mediterranean plant species evolved an array of physiological and morphological traits to cope with the seasonality of the Mediterranean climate. The selected traits by having an adaptive role, contribute to explain the plant fitness and distribution in the Mediterranean region (Gulías et al., 2002). The forecasted increase in air temperature and altered precipitation regimes in the Mediterranean basin (Giorgi and Lionello, 2008) will affect the energy, carbon, water and nutrients transactions between plants and the environment. Thus, climate change may act as a directional selection factor (Gutschichk and BassiriRad, 2003). Nowadays climate change speeds up and it could occur faster than the capacity of plant species to adapt (Ramírez-Valiente et al., 2009). In particular, an increase in the frequency and intensity of extreme climatic events such as heat waves or longer drought periods are expected for the Mediterranean area because of climate change (IPCC, 2014). In this context, plants will need to undergo rapid adjustments in their physiology and morphology (Nicotra et al., 2010) to persist and thrive under new climatic conditions.

Plant traits are a suitable tool for describing functional aspects of plants and their relations to environmental conditions (Verheijen et al., 2015). Among them, leaf mass area (LMA) is at the center of a nexus of covering traits affecting the plant functional ecology (Shipley, 1995; Wright et al., 2004; Niinemets, 2015). In fact, LMA has important functional implications being a pivotal trait in the carbon-fixation strategy (Wright and Westoby, 2002) generally scaling with the leaf biomass investment per unit of leaf area and as well as per unit of leaf mass (Niinemets, 1999, 2001; Gratani and Varone, 2006; Poorter et al., 2009; Puglielli et al., 2015). LMA varies in response to climatic fluctuations (Bertin and Gary, 1998; Gratani and Varone, 2006) through modifications in its components such as leaf thickness (LT) and leaf tissue density (LTD). Nevertheless, variations in LMA require more plant material to achieve a given leaf area for light interception and, hence, implies higher construction costs per unit leaf area (González-Zurdo et al., 2016). These costs arise from the negative relationship between LMA and instantaneous carbon assimilation (Reich et al., 1997; Niinemets and Sack, 2006; González-Zurdo et al., 2016; Niinemets, 2016), even if costs are payed-back in terms of leaf-longevity, which leads to important trade-offs between productivity and persistence (Reich, 2014; González-Zurdo et al., 2016). LMA can vary widely at the single-species level in response to differences in the harshness of the habitat (He et al., 2006; Messier et al., 2010). For example, Gratani and Varone (2006) consider LMA as a good indicator of the capacity of Mediterranean species to respond to total yearly

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https://doi.org/10.1016/j.jaridenv.2017.12.007
Received 31 January 2017; Received in revised form 12 June 2017; Accepted 13 December 2017
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rainfall decrease and air temperature increase. Despite many studies (e.g. Niinemets, 2001; Wright et al., 2004; Poorter et al., 2009) investigate the LMA response to climatic factors changing, little attention has been posed on how changes in LMA and its components may affect the photosynthesis responsiveness to environmental limiting factors such as high temperature.

The pronounced seasonal and inter-annual climatic variation in Mediterranean dry ecosystems has produced a diversity in plant phenological strategies (Gratani and Crescente, 1997; Lehmann et al., 2009). Specifically, three different leaf habitus were evolved: the evergreen sclerophyllous, the drought deciduous, and the drought semi-decidous (Flexas et al., 2014). These groups strongly differ in terms of LMA, leaf life-span and photosynthetic rates as well as in their drought resistance (Gratani and Varone, 2004a, 2004b, 2006).

In this context, the aim of our study was to summarize net photosynthesis responsiveness to air temperature of eight species co-existing in the Mediterranean maquis. In particular, the considered community is composed by evergreen sclerophyllous (including needle leaves species) and semi-deciduous species. Since LMA varies across leaf habitus, we expected a greater inter-annual variability in LMA and its components for evergreen sclerophyllous species. In fact, as they are characterized by a longer leaf life span it is supposed that they are more able to vary the leaf cost investments in response to changing environmental conditions.

2. Materials and methods

2.1. Study area and plant material

For this study the following species were selected: *Arbutus unedo*, *Cistus incanus*, *Erica arborea*, *Erica multiflora*, *Phillyrea latifolia*, *Pistacia lentiscus*, *Quercus ilex* and *Rosmarinus officinalis*. The study was carried out in Mediterranean maquis developing inside Castelporziano Estate (41°45′N, 12°26′E, Rome, Italy). The study area is characterized by a Mediterranean type of climate. The mean minimum air temperature of the coldest month (January) was 4.9 ± 0.9 °C, the mean maximum air temperature of the hottest month (August) was 31.7 ± 1.4 °C, and the annual mean air temperature was 16.5 ± 6.4 °C. Total annual rainfall was 853 mm, with most of it occurring in autumn and winter. Dry period was from the beginning of June to the end of August; it is characterized by 95 mm of total rainfall and by minimum and maximum air temperature of 18 and 32 °C, respectively (data from Castelporziano Meteorological Station for the period 2006-2016). A detailed description of the vegetation for the Mediterranean maquis is given in Gratani and Crescente (2000).

A multi-year dataset was created from our previously published data from 2001 to 2010 and included net photosynthetic rate per unit of leaf area (A_a, μmol m^{-2} s^{-1}), leaf mass area (LMA, mg cm^{-2}), leaf tissue density (LTD, mg cm^{-3}) and total leaf thickness (LT, μm).

According to our aim, to summarize the responsiveness of A_a to air temperature, monthly A_a averages (obtained from measurements for three consecutive days in each month) from March to July over the entire decade were retained. The selected period was established on the basis of the yearly seasonal A_a trends across the entire decade. In the used data sources (Table 1), in each sampling, measurements of A_a were obtained from 08:00 to 12:00 (one measure each hour) on fully expanded sun leaves of the selected shrubs (at least 10 per species) under natural conditions, on cloud-free days (PAR > 1000 μmol photon m^{-2} s^{-1}) to ensure that near-maximum daily photosynthetic rates were measured. Measurements were always carried out using the widely employed gas exchange analysers in an open system. In particular, ADC LCA4 (Hoddesdon, UK) was used in 2002 and 2010 while Ciras-1 (PP Systems, UK) from 2003 to 2006. During the measurements, shoots and leaves were retained in their natural orientation. Unlike A_a, morphological data covered only the period 2001-2004. According to Gratani and Varone (2006), this period was characterized by years (2001 and 2003) with severe drought periods alternated with relatively rainy years (2002 and 2004). This was a good test-bed to estimate the inter-annual variability of morphological leaf traits. According to our data sources (Table 1), the selected morphological traits were determined on 20 fully expanded sun leaves per plant and per species collected in June as follow: LMA was calculated by the ratio between leaf dry mass and one-sided leaf area, the latter obtained by Image Analysis System (Delta-T Devices, England); LT was determined on hand cut leaf sections and measured by light microscopy through an image analysis system (Lucia G Laboratory imaging LW-LUG from 2002 to 2006 and Axiovision AC software in 2010) on vein-free areas; LTD was determined by the ratio between LMA and LT (Wright et al., 2004). Despite the differences in the coverage of the years, we could relate the physiological dataset with the morphological one because no differences in terms of slopes and intercepts were found for the relationships A_a-T_M between the periods 2001-2004 and 2005-2010.

Thus, the dataset was composed of 176 observations (i.e. 22 per each species) for A_a, for the period 2001-2010, and 16 observations for LMA, LTD and LT for the period 2001-2004.

Among the climate variables, the mean maximum monthly air temperature (T_{max}), mean minimum monthly temperature (T_{min}), mean monthly temperature (T_M), relative air humidity (RH, %) and total monthly rainfall were used (data from Castelporziano Meteorological Station, Table 1).

2.2. Data analysis

To analyze the response of the selected species to air temperature during spring-summer, the slopes of the linear relationship A_a-T_M were estimated by standardized major axis estimation (SMA; Warton et al., 2006). This regression method allowed to test for species-specific differences in terms of slopes and intercepts with the Likelihood Ratio and Wald statistic, respectively. Multiple comparisons between regression slopes and intercepts of the grouping variable (species) were also performed by adjusting p values with the Sidak correction. All analyses were run with the R library SMATR (Warton et al., 2012).

A principal component analysis (PCA, correlation matrix) was used to identify the patterns of variation of LMA, LTD and LT across species. The obtained PC axes were then regressed against SA_a via linear regression analysis to evaluate which combination of traits explained the responsiveness (i.e. the slope of the linear regressions) of A_a to T_M (hereafter referred as SA_a). Linear regressions were also performed on

Table 1
Leaf traits and data sources used for the considered species.

Species	Leaf traits	Literature
A. unedo	LMA, LTD, LT, A_a	Gratani and Ghia (2002)
A. unedo, C. incanus, E. arborea, E. multifloraP. latifolia, P. lentiscus, Q. ilex, R. officinalis,	LMA, LTD, LT, A_a	Bertin and Gary (1998)
E. arborea, E. multiflora, R. officinalis	LMA, LTD, LT, A_a	Gratani and Varone (2004a)
A. unedo, C. incanus, E. arborea, E. multiflora,P. latifolia, P. lentiscus, Q. ilex, R. officinalis	A_a	Gratani and Varone (2004b)
Q. ilex, P. latifolia, P. lentiscus, A. unedo,C. incanus, E. arborea, E. multiflora, R. officinalis	LMA, LTD, LT, A_a	Gratani and Varone (2006)
Q. ilex, P. latifolia, P. lentiscus	A_a	Gratani and Varone (2006)
A. unedo, C. incanus, E. arborea, E. multiflora,P. latifolia, P. lentiscus, Q. ilex, R. officinalis	A_a	Catoni (2013)

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