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How water supply during leaf development drives water stress response in *Corylus avellana* saplings

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ABSTRACT

Corylus avellana L. (hazelnut) is one of the world's major nut crops, and is considered a sensitive species to water stress having a low capacity for stomatal regulation. Knowledge of hazelnut response to water stress is important from an economical point of view since water stress affects fruit quality and production. In this context, the effects of three different water regimes imposed during leaf development of hazelnut saplings were analyzed. The results suggested that saplings which formed leaves under moderate and severe-water stress regimes (MS and SS saplings, respectively) displayed several anatomical, morphological and physiological acclimations compared to those developed under a well-watered regime (WW saplings), giving them a greater capacity to cope with water stress. For instance, at a morphological level, MS and SS saplings had a higher leaf mass per unit of leaf area (LMA) and leaf tissue density (LTD) (by 15% and 36%, mean value, respectively) compared to WW saplings. At a physiological level, stressed SS and MS saplings show higher dark respiration rates (R_D), an improved photo-protection mechanism and a higher capacity to dissipate the excess of excitation energy (i.e. a higher carotenoid to chlorophyll ratio; a lower Φ_{PSII}) in respect to stressed WW saplings. During the imposed water stress, the 18% increase of the intrinsic water use efficiency (*i*WUE) in all three treatments attests to the stomatal control in the net assimilation rate (A_N) decrease. Taking into account that in the Mediterranean area supplemental irrigation in hazelnut orchards is required and that ground water supplies are declining while energy costs of irrigation are increasing, these results may provide important findings from an agricultural point of view concerning irrigation decisions about the water supply to hazelnut saplings.

1. Introduction

Under the context of climatic change, drought is becoming a real problem most constraining plant growth and ecosystem productivity in many regions all over the world, particularly in arid and semi-arid areas (Riccardi et al., 2016). Plants respond to water deficit with a down-regulation of photosynthesis which occurs through a decrease in stomatal conductance and/or mesophyll conductance (Flexas et al., 2006; Catoni and Gratani, 2014; Chastain et al., 2014), and in the biochemical efficiency (Flexas and Medrano, 2002; Lawlor and Cornic, 2002; Galmés et al., 2013). In particular, under drought events, down-regulation of the photosynthetic metabolism as a result of low stomatal conductance is the main limitation on photosynthesis (Flexas et al., 2006). Therefore, the drought effects on plants depends on the impact on plant at physiological, biochemical and molecular processes and on the ability of plant to adapt in these conditions (Massonnet et al., 2007). Plants developed a wide range of mechanisms in response to drought (Ha et al., 2014). In particular, leaf is the main organ which responds to environmental conditions (Nevo et al., 2000), thus its structure reflects the effects of water stress more clearly in respect to others organs such as stem and roots (Guerfel et al., 2009). Leaf anatomical traits variations determine differences in the CO_2 diffusion pathway from the sub-stomatal cavities to the site of carboxylation contributing to the maintenance of sufficient photosynthetic rates despite the low stomatal conductance (Evans and Loreto, 2000).

Corylus avellana L. (hazelnut) is one of the major world's nut crops (Boccacci et al., 2008) resulting second in nut production after almond (*Prunus amygdalus* Batsch) (Shahidi et al., 2007). To date, Turkey is the major world hazelnut producer (660,000 tons of dry in-shell nuts), accounting for about 72% of the world production, followed by Italy (85,232 tons), USA (30,000 tons), Azerbaijan (29,624 tons) and Georgia (24,700 tons) (FAO Production Yearbook 2012).

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Notation index

A_N	Net assimilation rates [μmol (CO_2) m^{-2} s^{-1}]
Chl $_{a+b}$	Total chlorophyll content [mg(Chl) leaf g^{-1}]
Car	Carotenoid content [mg(Car) leaf g^{-1}]
C_i	Sub-stomatal CO_2 concentration (ppm)
E	Transpiration rate [mmol (H_2O) m^{-2} s^{-1}]
ETR	Electron transport rates [μmol (electrons) m^{-2} s^{-1}]
ETR/A_N	Ratio between electron transport rates and net assimilation rate
F_v/F_m	Maximal quantum yield of *Psi*I photochemistry
g_s	Stomatal conductance [mol (H_2O) m^{-2} s^{-1}]
*i*WUE	Intrinsic water use efficiency [μmol (CO_2) mol (H_2O)$^{-1}$]
LMA	Leaf mass per unit of leaf area (mg cm^{-2})
LTD	Leaf tissue density (mg cm^{-3})
PPFD	Photosynthetic photon flux density [μmol (photons) m^{-2} s^{-1}]
R_D	Dark respiration rates [μmol (CO_2) m^{-2} s^{-1}]
R_D/A_N	Ratio between dark respiration rates and net assimilation rates
RWC_{pd}	Relative water content at pre-down (%)
SAI	Stomatal area index
SD	Stomatal density (n° stomata mm^{-2})
VPD	Vapor pressure deficit (KPa)
Φ_{PSII}	Effective quantum yield of PSII photochemistry
Ψ_{pd}	Leaf water potential at pre-down (MPa)

Hazelnut is considered a sensitive species to water stress by its low capacity of stomatal control (Bignami et al., 2009, 2011; Cristofori et al., 2014). Knowledge about hazelnut response to water stress is of importance from an economical point of view, since it affects fruit production and quality by determining early cessation of fruit growth, early leaf fall, blank nut increase, kernel decrease and a higher susceptibility to disease (Bignami et al., 2000; Diaz et al., 2005). For these reasons, hazelnut production is limited to those areas where rainfall meets crop water requirements (Marsal et al., 1997; Reis and Yomralioglu, 2006), specifically hazelnut needs about 800 mm of rainfall well distributed through the year (Cristofori et al., 2014). However, in the Mediterranean basin water shortage is one of the main growth-limiting factors for crop species (Martinelli et al., 2014). Therefore, supplemental irrigation in hazelnut orchards is necessary to minimize the impact of water stress on crop's performance in late spring and early summer, which is a crucial period to provide photosynthates for both fruit filling and reserve accumulation for the following year (Baldwin, 2009; Marsal et al., 1997; Solar and Stampar, 2011). In fact, according to the results obtained by Bignami et al. (2011) irrigation in hazelnut orchard improved yield and positively affected the kernel percentage in respect to not irrigated orchards. Nevertheless, the availability of water for irrigation purpose is declining due to the increase of domestic and industrial needs. In the same time, tourism in the Mediterranean areas increases during summer which coincides with the period of higher irrigation demand. This leads to a subsequent and additional over-extraction and lowering of the groundwater table (Garcia and Server, 2003). For these reasons a greater awareness of water needs of hazelnut in orchards is necessary in order to optimize the water supply, particularly in areas with limited water availability, irregular rain distribution during the year as well as in young plants (Cristofori et al., 2014). In this respects, several studies were carried out for analyzing the water needs of hazelnut in orchards (Bignami et al., 2009, 2011; Cristofori et al., 2014; Gispert et al., 2015). Moreover, a deeper knowledge of the mechanisms that regulate hazelnut carbon assimilation under water stress conditions is of great interest in the framework of agricultural management. In this context, the aim of the present research was to investigate the water stress effects on *C. avellana* cv. ‘Tonda Gentile Romana‘ saplings by experimentally withholding irrigation. In particular, saplings were subjected to different water regimes throughout the whole leaf development. We analyzed how different leaf traits determine a different capability to cope with water stress, considering that irrigation deficit affects some morphological and physiological traits related to the hardening of seedlings or saplings (Bañon et al., 2003).

2. Materials and methods

2.1. Study area and plant material

Experiments were carried out from March to July 2015 at the experimental garden of the Sapienza University of Rome (41°54′ N, 12°31′ E; 41 m a.s.l.). Two-year old saplings ($n = 60$) of *C. avellana* cv íTonda Gentile Romanaí (mean height and diameter = 58 ± 5 cm and 1.2 ± 0.1 cm, respectively) from the nursery near Viterbo (VT, 42°25′N, 12°06′E, Lazio) were growing in pots (diameter = 24 cm, volume = 9 L). Pots contained an organic commercial substrate (COMPO BIO, COMPO GmbH, Germany) with the following composition and hydrological properties: organic carbon (C) 35%, humic carbon 11%, organic nitrogen (N) 1.4%, carbon on total nitrogen ratio of 25, peat (65%), pH(H_2O) 6.0–7.0, bulk density 220 kg m^{-3}, field capacity 63% and permanent wilting point 33%.

The study site is characterized by a Mediterranean type of climate. The mean minimum air temperature (T_{min}) of the coldest months (January and February) is 4.9 ± 0.1 °C, the mean maximum air temperature (T_{max}) of the hottest months (July and August) 31.6 ± 0.2 °C and the yearly mean air temperature 16.6 ± 6.5 °C. Total annual rainfall is 866 mm most of it occurring in autumn and in winter. Dry period is from June to August (95 mm of total rainfall in this period) (mean value for the years 2006–2014). During the study period (March-July 2015) T_{min} of the coldest month (March) was 7.7 ± 1.3 °C and T_{max} of the hottest month (July) was 33.9 ± 1.3 °C associated to a total rainfall of 3 mm (data from Meteorological Station, Lanciani street, Rome, SIARL, Arsial, for the period 2006–2015).

2.2. Experimentally imposed water stress

At the beginning of March 2015 (i.e. at the time of leaf emergence) saplings were transferred in a greenhouse and randomly subjected to three different water regimes. In particular, twenty saplings were maintained at 100% of field capacity and, thus, considered as well-watered saplings (WW), twenty saplings were subjected to a moderate water stress (MS) and maintained at 50% of the field capacity, and twenty saplings to a severe-water stress (SS) and maintained at 25% of the field capacity. During this time all pots were daily weighted to evaluate the water loss. The imposed water stress experiment was carried out from July 6th to July 13th. All saplings were irrigated regularly according to the type of treatment until July 6th when the experiment started. A complete randomized design with ten replicates per treatment was established. In particular, ten replicates of each treatment were used as control (WW_C, MS_C and SS_C) and irrigated and ten replicates were subjected to water stress (WW_S, MS_S and SS_S). The water stress treatment was induced by withholding the irrigation until stomatal conductance was below 0.05 mol m^{-2} s^{-1} which was indicative of a severe water stress condition (Medrano et al., 2002). Thus, the last day of the experiment (day_L) was marked as the first day with g_s value below 0.05 mol m^{-2} s^{-1}. In the glasshouse microclimate measurements were carried over the study period. In particular, air temperature