DOI: 10.1007/s11099-015-0078-5 PHOTOSYNTHETICA 53 (1): 35-46, 2015

Corylus avellana responsiveness to light variations: morphological, anatomical, and physiological leaf trait plasticity

R. CATONI[*], M.U. GRANATA[**], F. SARTORI[**], L. VARONE[*], and L. GRATANI[*,+]

Department of Environmental Biology, Sapienza University of Rome, P.le A. Moro 5, 00185 Rome, Italy[*]
*Department of Earth and Environmental Sciences University of Pavia, Via S. Epifanio 14, 27100 Pavia, Italy[*]**

Abstract

Morphological, anatomical, and physiological leaf traits of *Corylus avellana* plants growing in different light conditions within the natural reserve "Siro Negri" (Italy) were analyzed. The results highlighted the capability of *C. avellana* to grow both in sun and shade conditions throughout several adaptations at leaf level. In particular, the more than 100% higher specific leaf area in shade is associated to a 44% lower palisade to spongy parenchyma thickness ratio compared with that in sun. Moreover, the chlorophyll (Chl) *a* to Chl *b* ratio decreased in response to the 97% decrease in photosynthetic photon flux density. The results highlighted the decrease in the ratio of Chl to carotenoid content, the maximum PSII photochemical efficiency, and the actual PSII photochemical efficiency (Φ_{PSII}) associated with the increase in the ratio of photorespiration to net photosynthesis (P_N) in sun. Chl *a*/*b* ratio was the most significant variable explaining P_N variations in shade. In sun, P_N was most influenced by the ratio between the fraction of electron transport rate (ETR) used for CO_2 assimilation and ETR used for photorespiration, by Φ_{PSII}, nitrogen content per leaf area, and by total Chl content per leaf area. The high phenotypic plasticity of *C. avellana* (PI = 0.33) shows its responsiveness to light variations. In particular, a greater plasticity of morphological (PI_m = 0.41) than of physiological (PI_p = 0.36) and anatomical traits (PI_a = 0.24) attests to the shade tolerance of the species.

Additional key words: leaf area; leaf respiration; leaf thickness; photorespiration.

Introduction

The environment can induce changes in the individual's behavior and such changes may be crucial to survival in heterogeneous and variable conditions (Pintado *et al*. 1997, Sultan 2000, Gratani *et al*. 2003, Zunzunegui *et al.* 2011). Phenotypic plasticity can be considered as the ability of an organism to express different phenotypes by altering plant traits in response to changes in the environmental conditions (Schlichting 1986). Since phenotypic plasticity influences environmental tolerance, the plant plastic responses may contribute to differences in the range of environments that species inhabit (Ackerly *et al*. 2000). Nevertheless, physiological and morphological plasticity may have a different role in plant adaption. In particular, physiological plasticity is more linked to an

Received 7 April 2014, *accepted* 2 June 2014.
[+]Corresponding author; phone/fax: +39 06 49912358, e-mail: loretta.gratani@uniroma1.it
Abbreviations: C – soil organic carbon content; C/N – ratio between carbon and nitrogen content; Chl – chlorophyll; Car – carotenoid content; C_i – substomatal CO_2 concentration; DM – dry mass; E – transpiration rate; ETR – electron transport rate; ETR_A – fraction of ETR used for CO_2 assimilation; ETR_P – fraction of ETR used for photorespiration; F_0 – minimal fluorescence yield of dark-adapted state; F_0' – minimal fluorescence yield of the light-adapted state; F_m – maximal fluorescence yield of the dark-adapted state; F_m' – maximal fluorescence yield of the light-adapted state; F_s – steady-state fluorescence yield; F_v/F_m – maximal quantum yield of PSII photochemistry; g_m – mesophyll conductance; g_s – stomatal conductance; LA – leaf area; L – total leaf thickness; N – total soil nitrogen content; N_a – leaf nitrogen content; PI – mean plasticity index; PI_a – anatomical plasticity index; PI_m – morphological plasticity index; PI_p – physiological plasticity index; P_N – net photosynthetic rate; PNUE – photosynthetic nitrogen use efficiency; P_r – photorespiration rates; R_D – respiration rate; RH – relative air humidity; SLA – specific leaf area; SOM – soil organic matter content; SWC – soil water content; T_a – air temperature; T_l – leaf temperature; T_m – mean air temperature; T_{max} – mean maximum air temperature; T_{min} – mean minimum air temperature; Φ_{PSII} – effective quantum yield of PSII photochemistry.
Acknowledgements: This work was supported by grants from the Department of Earth and Environmental Sciences, University of Pavia, for the project of "Caratterizzazioni funzionali e strutturali delle specie presenti nella Riserva Naturale Integrale Bosco Siro Negri".

enhanced capacity to colonize gaps and open areas (Niinemets and Valladares 2004) because it ensures instantaneous gas-exchange adjustments to stress factors (Zunzunegui *et al*. 2009). Moreover, a high physiological plasticity increases plant capability to colonize early successional habitats (Walters and Reich 1999). On the contrary, morphological plasticity is more linked to an enhanced capacity to survive and grow in forest understory (Valladares *et al*. 2002). A high degree of morphological plasticity is a part of the mechanism of resource acquisition (*i.e*. larger leaf area) in low-light environments (Navas and Garnier 2002, Herr-Turoff and Zedler 2007). Exploring morphological and physiological leaf traits in response to high and low light provides new insights into plant acclimation to contrasting light environments (Duan *et al.* 2005). In this context, the analysis of plasticity to shaded *vs*. open conditions provides an excellent system to examine plastic responses to specific environmental cues (Dorn *et al*. 2000).

Species with extensive geographical range show large intraspecific variations in physiology, morphology, and phenology and may be considered good models for the study of local and regional adaptations (Soolanayakanahally *et al.* 2009). Therefore, it is important to increase knowledge concerning phenotypic plasticity of species having an economic interest in order to obtain concrete baseline information on which base management raises productivity and yield.

The genus *Corylus* contains eleven recognized species disjunctly distributed in the Northern Hemisphere (Whitcher and Wen 2001). Among them, *C. avellana* is one of the world major nut crops (Boccacci *et al.* 2008) with world production totaling 888,328 Mt in 2010 (FAOSTAT 2012). This species is selected for large kernels of high quality (Bassil *et al*. 2005), second in nut production after almond (*Prunus amygdalus* Batsch) (Shahidi *et al*. 2007). To date, Turkey is the major world producer of *C. avellana* (430,000 t of dry, in-shell nuts) accounting for about 71% of world production, followed by Italy (128,940 t), USA (34,927 t), Azerbaijan (32,922 t), and Georgia (31,100 t) (FAO Production Yearbook 2011). In particular, in Italy, 68,000 ha are invested in *C. avellana* cultivation (means 2007–2011, FAOSTAT 2013) of which 98% of the producing surface is located in Campania (40%), Latium (33%), Piedmont (33%), and Sicily (14%) (Valentini *et al.* 2014). Several studies indicate that fat and mineral composition of *C. avellana* nut are affected by variety, geographical origin, climate, and methods of cultivation (Percerisa *et al.* 1995, Pershern *et al.* 1995). *C. avellana* has a wide geographical distribution in Europe in a large range of climates, from the Mediterranean coasts of North Africa northward to the British Islands and the Scandinavian Peninsula, and eastward to the Ural Mountains of Russia, Caucasus Mountains, Iran, and Lebanon (Kasapligil 1972). It is absent in Iceland, in some Mediterranean islands (Cyprus, Malta, and Baleari) and in northernmost and southernmost Europe (Kasapligil 1972). *C. avellana* grows on soils characterized by a pH from neutral to basic (Persson *et al.* 2004) and generally colonizes the understory of mixed deciduous forests (Pignatti 1982, Persson *et al*. 2004) being a shade-tolerant species (Kull and Niinemets1993, Gratani and Foti 1998). Nevertheless, it can grow also in full sunlight colonizing large gaps (Kull and Niinemets 1993, Niinemets *et al*. 1998).

In this context, the aim of the present research was to analyze morphological, anatomical, and physiological leaf trait variations of *C. avellana* plants growing in different light conditions within the Natural Reserve "Siro Negri". Taking into account the importance of nut production from *C. avellana* in Italy, knowledge on phenotypic plasticity may be of interest in order to analyze the species adaptation to different environmental conditions considering the wider ecological implications of plasticity for distribution, spread and persistence of this species.

Materials and methods

Study area and plant material: The study was carried out in a broadleaf deciduous forest within the natural reserve "Siro Negri" (45°12'39"N; 09°03'26"E, 74 m a.s.l., Italy) in the period of April–November 2013. The reserve extending over 10 ha represents one of the best conserved relicts of the original alluvial forests which in the past largely covered the banks of the Ticino river, and where no logging was carried out since the establishment of the reserve in 1970 (Sartori 1984, Castagneri *et. al*. 2013). The reserve belongs to a Site of Community Importance (IT 2080014, "Bosco Siro Negri and Moriano") which covers an area of 1,352 ha.

The climate of the area was characterized by a mean annual rainfall of 672 mm, most of it falling in spring and autumn. The mean minimum air temperature (T_{min}) of the coldest month (January) was –0.3 ± 1.7°C, the mean maximum air temperature (T_{max}) of the hottest month (July) was 30.0 ± 1.3°C, and the mean annual temperature (T_m) was 13.7 ± 8.2°C. During the study period, total rainfall was 507 mm, T_m was 18.0 ± 5.6°C, and T_{max} (July) was 28.4 ± 1.2°C (Lombardia Regional Agency for Environmental Protection, Meteorological Station of Pavia, Ponte Ticino SS35, data for the period 2002–2013). Floods occurred sporadically every 5–10 years during the last 40 years, with water levels up to 1.5 m height in the forest during exceptional events (Motta *et al*. 2009, Castagneri *et al.* 2013). On an average, groundwater level was around –4.5 m in winter, reaching –3.5 m in summer due to irrigation in the surrounding areas.

Five representative *C. avellana* plants growing in high-light conditions, outside the forest (sun plants) and five plants growing in the understory of the forest (shade plants) were selected:

Parameter	Sun plants	Shade plants
Mean height [m]	3.0 ± 0.5	2.15 ± 1.20
Basal diameter [cm]	4.7 ± 2.1	8.8 ± 1.9
Crown volume [m^3]	15.7 ± 2	3.1 ± 0.9
Number of stumps	6 ± 2	7 ± 1

Soil and microclimate measurements: Soil samples (500 g each, three samples for each sun and shade conditions) were collected in the area of the selected plants at the beginning of November, at least 5 days after the last rainfall, by a hand auger at 40-cm depth. Soil analysis was performed according to Violante (2000): pH, soil water content (SWC), total soil nitrogen content (N), soil organic matter content (SOM), and soil organic carbon content (C) were determined. Soil samples were air-dried and then passed through a 2-mm sieve. The pH (in H_2O) was measured by a glass electrode pH meter (*Corning Model 220 pH-meter, Labequip Ltd.,* Canada) on a 1:2.5 soil–water suspension. N was determined by the Kjeldahl method, and C by the oxidation method using $K_2Cr_2O_7$-H_2SO_4 (Sims and Haby 1971). The ratio between carbon and nitrogen content (C/N) was calculated. SWC was determined on soil samples (500 g each) as fresh soil minus dry soil divided by dry soil, calculated after oven-dried at 90ºC to a constant mass.

Microclimate measurements were carried out monthly during the study period from 09.00 to 12.00 h, in the forest understory (shade) and in the open area (sun). In particular, the PPFD was measured by a quantum radiometer photometer (*LI-185B, Licor*, USA). Relative air humidity (RH) and air temperature (T_a) were measured by thermo-hygrometer (*HD8901, Delta Ohm*, Italy).

Morphological and anatomical measurements: Fully expanded leaves (n = 10 per each sun and shade plants) from the external medium portion of the crown of the considered plants were collected at the end of May. Leaf samples were sealed in plastic bags and transported immediately to the laboratory for measurements. Measurements included leaf surface area (LA), obtained by the image analysis system (*Delta-T Devices*, UK) and leaf dry mass (DM), determined by drying leaves at 80°C to constant mass. The specific leaf area (SLA) was calculated by the ratio of LA and DM.

Fresh leaf sections from fully expanded leaves (n = 5 per each sun and shade plants) were hand cut and analyzed by light microscopy using an image analysis system (*Axiovision AC software*). The following parameters were measured: total leaf thickness (L), palisade and spongy parenchyma thickness, adaxial and abaxial epidermis, and cuticle thickness. All measurements were restricted to vein-free areas, according to Chabot and Chabot (1977).

Gas-exchange measurements were carried out in the period of April–November 2013 (three leaves per each sun and shade plant). Leaves were retained in their natural position during measurements. Net photosynthetic rate (P_N), stomatal conductance (g_s), leaf transpiration (E), PPFD, leaf temperature (T_l), and substomatal CO_2 concentration (C_i) were measured by an infrared gas analyzer (*LCA-Pro, ADC*, UK) equipped with a leaf chamber (*PLC*, *Parkinson Leaf Chamber*, UK). Measurements were carried out on cloud-free days in the morning from 9.00 to 12.00 h. In particular, measurements in sun were carried out when PPFD was ≥ 1,200 μmol(photon) m^{-2} s^{-1} to ensure that the maximum rates were measured (Hampson *et al.* 1996).

On each sampling occasion, leaf respiration (R_D) was measured after P_N measurements (on the same leaves) as CO_2 efflux by darkening the leaf chamber with a black paper, according to Cai *et al*. (2005) for 30 min prior to each measurement, to avoid the release of CO_2 transient postirradiation bursts (Atkin *et al*. 1998). The shown R_D and P_N represented the mean values of three days of measurements per month characterized by the same weather conditions. The ratio between R_D and P_N was calculated.

Chl fluorescence and mesophyll conductance: Chl fluorescence measurements were carried out by a portable modulated fluorometer (*OS5p, Opti-Sciences*, USA). Maximum PSII photochemical efficiency (F_v/F_m) was estimated by darkening leaves (three leaves per each sun and shade plants) for 20 min, then a saturating pulse was applied to measure initial (F_0) and maximum (F_m) fluorescence. F_v/F_m was estimated as: $(F_m - F_0)/F_m$.

Additional gas-exchange and Chl fluorescence measurements were made on leaves (three leaves per each sun and shade plant) comparable to those previously used in order to estimate mesophyll conductance (g_m). The g_m was calculated according to Harley *et al*. (1992) by a single-point method which combines gas-exchange and Chl *a* fluorescence measurements, as:

$$g_m = P_N/\{C_i - [\Gamma^* \times [ETR + 8 \times (P_N + R_D)]]/ [ETR - 4 \times (P_N + R_D)]\}$$

where Γ^* was the CO_2 compensation point under nonrespiratory conditions. The temperature dependency for Γ^* was calculated according to Bernacchi *et al*. (2002). P_N, C_i, and R_D were obtained from gas-exchange measurements as described in the above section. ETR was the electron transport rate calculated from Chl fluorescence measurements, according to Krall and Edwards (1992) as:

$$ETR = \Phi_{PSII} \times PPFD \times 0.5 \times 0.84,$$

where Φ_{PSII} was the actual PSII photochemical efficiency of light-adapted leaves calculated according to Genty *et al*. (1989) as: $(F_m' - F_s)/F_m'$. F_m' was the maximum fluorescence obtained with a light-saturating pulse (~8,000 μmol m^{-2} s^{-1} PPFD) and F_s was the steady-state fluorescence of

illuminated leaves (1,500 μmol m^{-2} s^{-1} PPFD).

Gas-exchange and Chl fluorescence measurements were taken concurrently by fitting the portable infrared CO_2 gas analyzer with a fluorometer adapter chamber (*F.LCI-FL*, *ADC*, UK). The measured ETR can be divided into two components: ETR = ETR_A+ ETR_P, where ETR_A represents the fraction of ETR used for CO_2 assimilation and ETR_P is the fraction of ETR used for photorespiration. These values can be solved from data of P_N, R_D, and ETR, and from the known stochiometries of electron use in photosynthesis and photorespiration, according to Epron *et al*. (1995) as follows:

$$ETR_A = 1/3 \times [ETR + 8 \times (P_N + R_D)]$$
$$ETR_p = 2/3 \times [ETR - 4 \times (P_N + R_D)]$$

where the ratio ETR_A/ETR_P, indicative of the fraction ETR devoted to CO_2 assimilation, was calculated according to Valentini *et al.* (1995).

Photorespiration measurement: The photorespiration (P_r) was calculated from the combined gas-exchange and Chl fluorescence measurements assuming that all the reducing power generated by the electron transport chain was used for photosynthesis and photorespiration, and that Chl fluorescence gave a reliable estimation of the quantum yield of electron transport, according to Valentini *et al.* (1995). Accordingly, P_r was solved from P_N, R_D, and ETR and the known stochiometries of electron use in photorespiration, as follows:

$$P_r = 1/12 \times [ETR - 4 \times (P_N + R_D)].$$

The ratio P_r/P_N was calculated.

Leaf nitrogen and photosynthetic pigment contents were measured in leaves collected at the same occasions of gas-exchange measurements. Immediately after collection, leaf samples were kept cool in the dark and transported immediately to the laboratory. Leaf N [N_a, g(N) m^{-2}] content was determined by drying leaf samples at 70°C (six samples, 0.5 g of leaf dry mass each, per sun and shade plants, respectively, and per each occasion) grounding them into a fine powder. The N was measured by the Kjeldahl method (Mendes *et al*. 2001). Photosynthetic nitrogen-use efficiency (PNUE) was calculated by the ratio between P_N rates and N_a.

Chl and carotenoid (Car) contents were determined after grinding leaves in acetone (six samples, 1.5 g of leaf fresh mass each, per sun and shade plants, respectively, per each occasion). The homogenates were centrifuged in a refrigerated centrifuge (*4237R., A.L.C.*, Italy). The absorbance of the supernatants was measured by a spectrophotometer *7800LCD* (*Jasco,* Japan) at the wavelengths of 645, 663, and 440 nm for Chl *a*, Chl *b*, and Car, respectively. Chl content was calculated according to Maclachlan and Zalik (1963) and Car content according to Holm (1954). The Chl (*a*+*b*) content, the ratio Chl *a*/*b*, the ratio Chl/Car, and the ratio Chl/N were calculated.

Leaf plasticity: The plasticity index was calculated for each of the considered anatomical (PI_a), morphological (PI_m), and physiological (PI_p) leaf traits measured in May, as the difference between the minimum and the maximum mean value between sun and shade leaves divided by the maximum mean value, according to Valladares *et al*. (2000). The mean plasticity index (PI) was calculated by averaging the plasticity index for all the considered anatomical, morphological, and physiological leaf traits.

Statistical analysis: All statistical tests were performed using a statistical software (*Statistica, Statsoft*, USA). Differences in morphological, anatomical, and between soil parameters were analyzed by one-way analysis of variance (*ANOVA*). Repeated measure *ANOVA* was performed on physiological variables to test for significant difference ($p \leq 0.05$) among months (*i.e.* main factor) and sampling days (*i.e.* within effect) in sun and shade plants.

Simple regression analysis was carried out among the considered leaf traits. A multiple regression analysis was carried out to investigate the influence of physiological leaf traits on photosynthesis both in sun and shade, by employing P_N as the dependent variable and N_a, Chl (*a*+*b*), Chl/N_a, Chl *a*/*b*, g_s, g_m, ETR_A/ETR_P, and Φ_{PSII} as independent variables.

Results

Soil and microclimate: The pH was 5.43 ± 0.04 and 5.46 ± 0.11 in sun and shade, respectively, and SWC was 18.7 ± 1.5% and 26.3 ± 3.9% in sun and shade, respectively. The soil N content was 50% higher in sun than in shade, while the ratio C/N was 99% higher in shade than in sun. SOM was 3.6 ± 0.5% and 4.4 ± 0.1% in sun and shade, respectively (Table 1). PPFD was 1,410 ± 178 and 36 ± 18 μmol(photon) m^{-2} s^{-1} (mean value of the study period) in sun and shade, respectively. On an average, T_a was 22.8 ± 5.4°C in sun decreasing by 14% in shade, whereas RH was 63± 6% in shade conditions decreasing by 24% in sun.

Leaf morphology and anatomy: There were significant differences between morphological and anatomical leaf traits for plants in sun and shade (Tables 2, 3). In particular, LA and SLA were 90% and more than 100% higher in shade than in sun, respectively. L was 26% higher in sun than in shade, and the ratio palisade to spongy parenchyma thickness was 44% lower in shade than in sun. Adaxial and abaxial epidermis were 8.9 ± 0.6 μm and 6.5 ± 0.9 μm, respectively, in sun and 6.7 ± 0.8 μm and 5.1 ± 0.4 μm, respectively, in shade. Leaves of plants in sun had a 27% (mean value) higher adaxial and abaxial cuticle thickness compared to plants in shade.

Table 1. Soil characterization in sun and shade conditions. SWC – soil water content; N – total soil nitrogen content; C/N – ratio between carbon and nitrogen content; SOM – soil organic matter content. Mean values (± SE) are shown (n = 3). *Different letters* indicate significant differences between sun and shade condition (t-test, p<0.05).

Parameter	Sun	Shade
SWC [%]	18.7 ± 1.5^a	26.3 ± 3.9^b
pH	5.43 ± 0.04^a	5.46 ± 0.11^a
N [%]	0.24 ± 0.02^a	0.16 ± 0.01^b
C/N	8.6 ± 2.1^a	17.1 ± 0.9^b
SOM [%]	3.6 ± 0.5^a	4.4 ± 0.1^a

Table 2. Morphological leaf traits of sun and shade plants of *Corylus avellana*. LA – leaf area; DM – dry mass; SLA – specific leaf area. Mean values (± SD) are shown (n = 50 leaves). *Different letters* indicate significant differences between sun and shade plants (t-test, p<0.05).

Parameter	Sun	Shade
LA [cm^2]	41 ± 6^a	78 ± 11^b
DM [mg]	263 ± 66^a	212 ± 44^b
SLA [$cm^2\ g^{-1}$]	163 ± 28^a	372 ± 38^b

Table 3. Anatomical leaf traits of sun and shade plants of *Corylus avellana.* Mean values (± SD) are shown (n = 25). *Different letters* indicate significant differences between sun and shade plants (t-test, p<0.05).

Leaf traits	Sun	Shade
Leaf thickess [µm]	97.6 ± 8.9^a	77.7 ± 4.9^b
Palisade parenchyma thickness [µm]	38.3 ± 2.7^a	21.9 ± 1.6^b
Spongy parenchyma thickness [µm]	43.4 ± 9.0^a	42.7 ± 4.3^a
Adaxial epidermides thickness [µm]	8.9 ± 0.6^a	6.7 ± 0.8^b
Adaxial cuticle thickness [µm]	0.8 ± 0.1^a	0.7 ± 0.1^b
Abaxial epidermides thickness [µm]	6.5 ± 0.9^a	5.1 ± 0.4^b
Abaxial cuticle thickness [µm]	0.7 ± 0.1^a	0.5 ± 0.1^b
Palisade to spongy parenchyma ratio	0.92 ± 0.22^a	0.52 ± 0.07^b

Gas-exchange measurements: The highest P_N were reached in May both in sun and shade [8.7 ± 0.5 and 4.1 ± 0.5 µmol(CO_2) m^{-2} s^{-1}, respectively] decreasing by 57% and 47%, respectively, in November during leaf senescence (Fig. 1). The highest g_s values for both sun and shade were measured in November, and the values were more than 100% higher than those monitored in May [0.21 ± 0.01 and 0.15 ± 0.01 mol(H_2O) m^{-2} s^{-1}, in sun and shade, respectively] (Fig. 2). The ratio R_D/P_N was the highest in November both in sun and shade (0.39 ± 0.08 and 0.76 ± 0.18, respectively) due to the lowest P_N associated to relatively high R_D [1.39 ± 0.13 and 1.58 ± 0.25 µmol(CO_2) m^{-2} s^{-1}, respectively] (Fig. 3). PNUE was the highest in May [6.1 ± 0.5 and 5.8 ± 0.7 µmol(CO_2) g^{-1}(N) s^{-1}, in sun and shade, respectively] decreasing by 34% and 36%, respectively, in November.

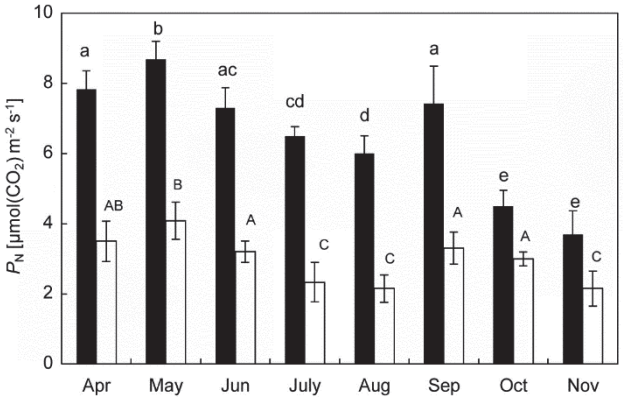

Fig. 1. Values of net photosynthetic rates (P_N) in sun plants (*filled bars*) and shade plants (*open bars*) during the study period. *Lowercase* and *capital letters* indicate differences in sun and shade plants, respectively. The means with *the same letters* are not significantly different. Differences between sun and shade plants in each month are significant (repeated measure *ANOVA*, $p \geq 0.05$). Mean values (± SD) are shown (n = 45).

Mesophyll conductance and Chl fluorescence: The highest g_m values were measured in May both in sun and shade [0.057 ± 0.008 and 0.027 ± 0.009 mol(CO_2) m^{-2} s^{-1}, respectively] and the lowest ones in November [0.0091 ± 0.0017 and 0.0010 ± 0.0003 mol(CO_2) m^{-2} s^{-1}, respectively] (Fig. 2).

F_v/F_m and Φ_{PSII} were significantly lower in sun than in shade during the study period (Fig. 4).

Photorespiration measurements: The ratio P_r/P_N was the lowest in May (2.4 ± 0.3) in sun, increasing more than 100% in November. An opposite trend was observed in shade, with the highest values in May (0.69 ± 0.22) and the lowest ones in November (0.13 ± 0.09). The ratio ETR_A/ETR_P was 87% (mean value of the study period) lower in sun than in shade.

Leaf nitrogen and pigment content: Nitrogen and pigment contents are shown in Table 4. The highest N_a content was measured in May both in sun and in shade [1.42 ± 0.04 and 0.70 ± 0.01 g(N) m^{-2}, respectively, and the lowest content in November [0.92 ± 0.05 and 0.58 ± 0.06 g(N) m^{-2}, respectively]. The Chl (a + b) content also had the highest values in May [0.047 ± 0.005 and 0.031 ± 0.004 g(Chl) m^{-2}, in sun and shade, respectively] decreasing by 62% and 35%, respectively, in November. The ratio Chl/Car decreased by 61% and 40% from May to November in sun and shade, respectively, and the ratio Chl/N_a by 43% and 18% in the same period, plants in shade showing a 45% (mean value) higher Chl/N_a compared to plants in sun.

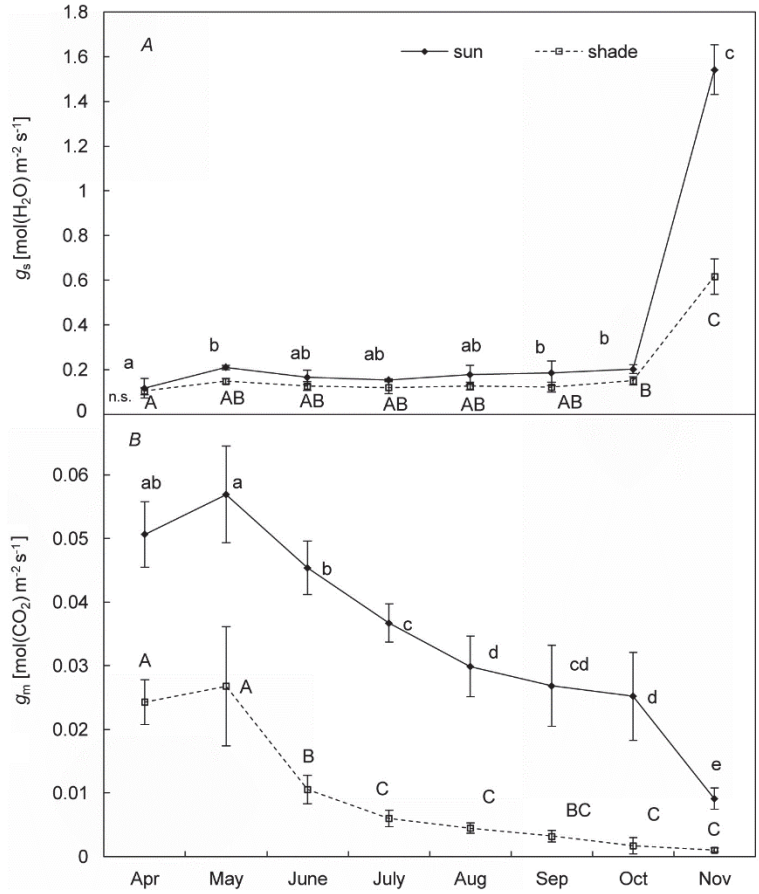

Fig. 2. Trend of (*A*) stomatal conductance (g_s) and (*B*) mesophyll conductance (g_m) during the study period in sun and shade plants. *Lowercase* and *capital letters* indicate differences in sun and shade plants, respectively. The means with *the same letters* are not significantly different. Differences between sun and shade plants in each month are significant (repeated measure *ANOVA*, $p \geq 0.05$) except when indicated (n.s. – not significant). Mean values (± SD) are shown ($n = 45$ for g_s; $n = 15$ for g_m).

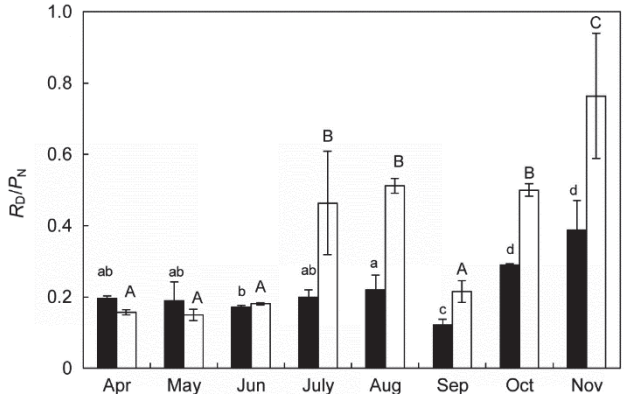

Fig. 3. Values of leaf respiration to net photosynthesis ratio (R_D/P_N) in sun plants (*filled bars*) and shade plants (*open bars*) during the study period. *Lowercase* and *capital letters* indicate differences in sun and shade plants, respectively. The means with *the same letters* are not significantly different. Differences between sun and shade plants in each month are significant (repeated measure *ANOVA*, $p \geq 0.05$). Mean values (± SD) are shown (n =45).

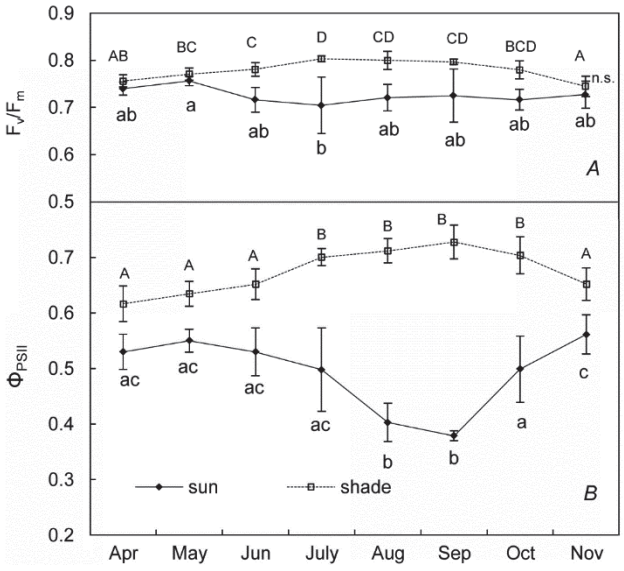

Fig. 4. Trend of (*A*) maximal quantum efficiency of PSII (F_v/F_m) and (*B*) the actual PSII photochemical efficiency (Φ_{PSII}) during the study period in sun and shade plants. *Lowercase* and *capital letters* indicate differences in sun and shade plants, respectively. The means with *the same letters* are not significantly different. Differences between sun and shade plants in each month are significant (repeated measure *ANOVA*, $p \geq 0.05$) except when indicated (n.s. – not significant). Mean values (± SD) are shown (n =45).

Table 4. Nitrogen and photosynthetic pigment content of *Corylus avellana* sun and shade leaves. N_a – leaf nitrogen content per unit of leaf area; Chl (*a*+*b*) – chlorophyll *a* + *b* per unit of leaf area; Chl *a*/*b* – chlorophyll *a* to chlorophyll *b* ratio; Chl/Car – chlorophyll to carotenoid ratio; Chl/N_a – chlorophyll to nitrogen ratio. Mean values (±SD) are shown (n = 18). *Lowercase letters* indicate differences between May and November in sun and shade plants. *Capital letters* indicate differences between sun and shade plants within each month. The means with *the same letters* are not significantly different (repeated measure *ANOVA*, $p \geq 0.05$).

Parameter	May		November	
	Sun	Shade	Sun	Shade
N_a [g(N) m^{-2}]	1.42 ± 0.04^{aA}	0.70 ± 0.01^{aB}	0.92 ± 0.05^{bA}	0.58 ± 0.06^{bB}
Chl (*a*+*b*) [g(Chl) m^{-2}]	0.047 ± 0.005^{aA}	0.031 ± 0.004^{aB}	0.018 ± 0.003^{bA}	0.020 ± 0.005^{bB}
Chl *a*/*b*	2.12 ± 0.39^{aA}	2.08 ± 0.07^{aA}	3.06 ± 0.28^{bA}	2.17 ± 0.80^{aB}
Chl/Car	6.16 ± 0.90^{aA}	6.43 ± 0.53^{bA}	2.42 ± 0.42^{aA}	3.88 ± 0.74^{bB}
Chl/N_a	0.035 ± 0.007^{aA}	0.044 ± 0.005^{aB}	0.020 ± 0.005^{bA}	0.036 ± 0.008^{bB}

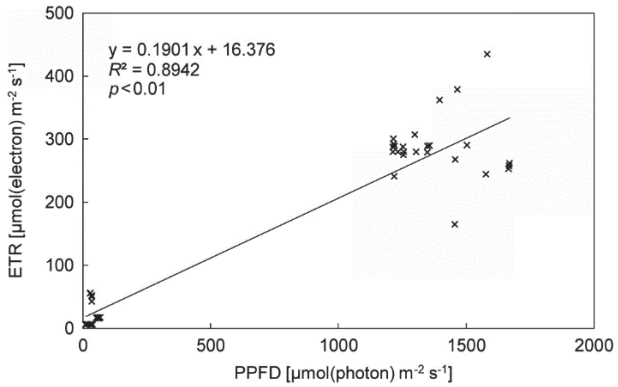

Fig. 5. Simple regression analysis between electron transport rate (ETR) and photosynthetic photon flux density (PPFD). The regression equation, determination coefficient (R^2), and *p*-value are shown.

Statistical analysis and phenotypic plasticity: The regression analysis showed a negative relationship between SLA and L (r = –0.83), and between Chl/N_a and PPFD (r = –0.56) and a positive relationship between N_a content and PPFD (r = 0.88). There was a positive (r = 0.94) relationship between ETR and PPFD (Fig. 5).

The results of the multiple regression analysis showed that N_a, Chl (*a*+*b*), ETR_A/ETR_p, and Φ_{PSII} were the variables which most explained P_N variations in sun and Chl *a*/*b* in shade (Table 5).

The PI of *C. avellana* was 0.33. In particular, PI_m (0.41) was higher than PI_p (0.36) and PI_a (0.24) (Table 6). SLA had the highest plasticity (0.56) among the considered morphological leaf traits, ETR (0.82) among physiological traits, and palisade to spongy parenchyma ratio (0.44) among anatomical traits.

Discussion

The results on the whole highlight the successful ability of *C. avellana* to grow in shade as well as in sun through several adaptations at morphological, anatomical, and physiological levels. With concern to the soil characteristics, there were no significant differences in the pH under sun and shade (5.43 ± 0.04 and 5.46 ± 0.11, respectively) while N content was 50% higher in sun than in shade, resulting in the range founded by Adiloglu and Adiloglu (2004) for the same species in Turkey. The ratio C/N is 99% higher in shade than in sun highlighting the higher C pools in the understory of the forest related to the larger amount of dead wood and litter.

During the study period, *C. avellana* P_N peaks in May [8.7 ± 0.5 and 4.1 ± 0.5 µmol(CO_2) m^{-2} s^{-1}, for sun and shade plants, respectively] when air temperature is favorable (ranging from 18 to 24°C), according to the results of Schulze and Küppers (1979) for the same species. The ratio R_D/P_N can be considered a simple approach to the leaf carbon balance because it indicates the percentage of photosynthates that are respired (Loveys *et al*. 2002). In particular, in this period the low ratio R_D/P_N (0.19 ± 0.05 and 0.15 ± 0.02, for sun and shade, respectively) highlights the lower proportion of carbon respired compared to that assimilated when resources are not limited and leaves take in roughly three to five times more CO_2 than they lose by the dissimilatory process (Larcher 2003). P_N decreased in November (by 57% and 47% for sun and shade, respectively) during leaf senescence. In this period a more than 100% higher g_s both in sun and shade may be related to a reduced stomatal responsiveness, according to the results of Grassi and Magnani (2005) and Matos *et al*. (2012) for other deciduous species. The reduced stomatal control to CO_2 diffusion is attested by the high substomatal CO_2 concentration in sun and shade plants. Nevertheless, taking into account that g_m regulates CO_2 diffusion from the substomatal cavity to the sites of Rubisco (de Lucia *et al.* 2003), the P_N decreasing during leaf senescence could be mainly due to a lower g_m [0.0091 ± 0.0017 and 0.0010 ± 0.0003 mol(CO_2) m^{-2} s^{-1}, in sun and shade plants, respectively].

Table 5. Results of the multiple regression analysis using net photosynthesis (P_N) as dependent variable and chlorophyll to nitrogen content ratio (Chl/N_a), Chl *a*/*b*, stomatal conductance (g_s), mesophyll conductance (g_m), ratio of the electron transport rates for CO_2 assimilation and for photorespiration (ETR_A/ETR_P), actual PSII photochemical efficiency (Φ_{PSII}), leaf nitrogen content per unit of leaf area (N_a), Chl (*a*+*b*) as independent variables. *Bold font* indicates variables which are significant ($p<0.05$). Multiple *R* value, intercept value, standardized (B coefficient), unstandardized (β coefficient) regression coefficient and *p*-level are shown.

Independent variables		Chl_a/N_a	Chl *a*/*b*	g_s	g_m	ETR_A/ETR_P Φ_{PSII}	N_a	Chl (*a*+*b*)
Sun								
Multiple *R* value	0.988							
Intercept	–72.485							
B regression coefficient		–6.895	0.376	1.372	–13.947	**96.715**	**53.709**	**–9.025**	**–150.939**
β regression coefficient		–0.074	0.246	0.048	–0.178	**2.685**	**1.849**	**–0.638**	**1.225**
p-level		>0.05	>0.05	>0.05	>0.05	**<0.05**	**<0.05**	**<0.05**	**<0.05**
Shade								
Multiple *R* value	0.922							
Intercept	–26.606							
B regression coefficient		–553.504	**5.414**	20.546	60.255	1.754	0.559	27.342	550.910
β regression coefficient		–4.536	**0.99**	0.599	1.021	1.045	0.047	1.197	3.497
p-level		>0.05	**<0.05**	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05

With regards to *C. avellana* response to sun and shade, the more than 100% higher SLA in shade is due to a 20% lower L as attested by the negative correlation between SLA and L because the larger and thinner shade leaves are more advantageous for light capture in low-light conditions (Gratani and Foti 1998). Moreover, a 44% reduced ratio of palisade to spongy parenchyma thickness in shade scatters irradiance internally increasing light absorption (Sack *et al*. 2006). On the contrary, the higher palisade parenchyma thickness of sun leaves provides a better light penetration to the chloroplasts (Duan *et al.* 2005). Changes in composition of pigments in response to varying light conditions lead to a successful acclimation in the growth irradiance. In particular, a 18% lower Chl *a*/*b* ratio in shade is determined by a higher Chl *b* content. This contributes to *C. avellana* acclimation to shade since Chl *b* is the main component of the LHC protein (Koike *et al*. 2001) which acts as an antenna complex in transferring light energy to the reaction centre of PSII (Lam *et al*. 1984). Accordingly, shade leaves can trap more light energy through LHCII to promote a higher photosynthetic efficiency (Huang *et al.* 2011). On the contrary, leaves in sun plants have relatively low Chl *b* content (*i.e*. higher Chl *a*/*b* ratio) and, in turn, a low light-trapping ability in the antennae of LHC. Through this mechanism more light energy can be dissipated as heat and fluorescence avoiding severe damage to reaction centres (Iglesias-Prieto and Trench 1997, Bailey *et al.* 2004).

It is known that P_N responses may be related to changes in leaf N_a, and N partitioning within leaves changes with growth irradiance in such a way to maximize photosynthesis (Evans and Poorter 2001). In this context, the ratio Chl/N_a which is indicative of N allocation to the Chl-protein complexes in the light-harvesting component at the expense of investment in other compounds (*e.g*. Rubisco) (Poorter *et al*. 2000) is 45% higher in shade than in sun. The Chl/N_a ratio is particularly important in a forest understory as nitrogen availability is crucial in determining plant capability to tolerate low irradiance (Niinemets 1997). Moreover, the lower N_a in shade leaves leads to a larger surface area with the same investment of plant N in leaf production, which is beneficial for improving light interception (Duan *et al*. 2005). On the contrary, leaves in sun have a 10% higher PNUE because of the more N allocated in the form of photosynthetic proteins which results in increased carboxylating enzymes (Rubisco) (Reich *et al.* 1995) responsible for the photosynthetic electron transport (Reich *et al.* 1995) as confirmed by the close and positive ($r = 0.94$) relationship between ETR and PPFD. The lower R_D/P_N ratio in sun is justified by more than 100% higher P_N and 38% higher R_D, with this last being necessary for a higher maintenance cost of the photosynthetic tissues (Pearcy and Sims 1994). On the contrary, the higher R_D/P_N in shade is due to the reduced R_D that allows the maintenance of a positive carbon balance (Givnish 1988, Amthor 2000). It is well known that in high-light conditions photoprotection mechanisms are needed in order to avoid photoinhibition (Matos *et al*. 2009, Moraes *et al*. 2010). Protection of photosynthesis from light stress in the natural environment is provided *via* the thermal dissipation of excess energy in PSII (Demmig-Adams and Adams 1996). The ratio F_v/F_m can be used as a sensitive indicator of the plant photosynthetic performance (Huang *et al*. 2011) with optimal values around 0.83 measured for plant species (Björkman and Demmig 1987, Johnson *et al.* 1993). The resulting F_v/F_m values (0.73 ± 0.02 and 0.78 ± 0.02, in sun and shade, respectively) highlight an efficient functioning of the photoprotection mechanism without oxidative damage to the photosynthetic machinery, as suggested by Demmig-Adams *et al.* (1996) and Thiele *et al*. (1998). A lower Φ_{PSII} in sun leaves compared to shade leaves

Table 6. Plasticity index for the anatomical, morphological, and physiological leaf traits of *Corylus avellana*. The anatomical (PI_a), morphological (PI_m), physiological (PI_p), and the mean plasticity indexes (PI, mean of PI_a, PI_m, and PI_p) are shown. P_N – net photosynthetic rate; R_D – respiration rate; R_D/P_N – ratio between R_D and P_N; g_s – stomatal conductance; g_m – mesophyll conductance; P_r/P_N – ratio between photorespiration and P_N; E – transpiration rate; PNUE – photosynthetic nitrogen use efficiency; N_a – leaf nitrogen content per unit of leaf area; Chl – chlorophyll; Car –carotenoid; N_a – nitrogen content; F_v/F_m – maximal quantum yield of PSII photochemistry; ETR – electron transport rate; ETR_A – electron transport rate for CO_2 assimilation; ETR_P – electron transport rate for photorespiration; Φ_{PSII} – effective quantum yield of PSII photochemistry; LA – leaf area; DM – dry mass; SLA – specific leaf area. *Bold font* indicates leaf traits that significantly differed ($p<0.05$) between sun and shade leaves.

Physiological leaf traits	Plasticity index
P_N	**0.53**
R_D	**0.63**
R_D/P_N	**0.22**
g_s	**0.31**
g_m	**0.53**
P_r/P_N	**0.71**
E	**0.41**
PNUE	0.05
N_a	**0.51**
Chl *a*/*b*	0.12
Chl (*a*+*b*)	**0.34**
Chl/Car	**0.04**
Chl/N_a	**0.21**
F_v/F_m	**0.02**
ETR	**0.82**
ETR_A/ETR_P	**0.47**
Φ_{PSII}	**0.15**
Mean PI_p	0.36
Morphological leaf traits	
LA	**0.47**
DM	**0.19**
SLA	**0.56**
Mean PI_m	0.41
Anatomical leaf traits	
Total leaf thickness	**0.20**
Palisade parenchyma thickness	**0.43**
Spongy parenchyma thickness	0.01
Upper epidermides thickness	**0.24**
Lower epidermides thickness	**0.20**
Upper cuticles thickness	**0.16**
Lower cuticles thickness	**0.22**
Palisade to spongy parenchyma ratio	**0.44**
Mean PI_a	0.24
PI	**0.33**

highlights their higher capacity to dissipate the excess of the excitation energy as heat (Björkman and Demmig-Adams 1994). Plants in sun can protect themselves from excessive absorbed light through the downregulation of photochemical efficiency by the xanthophyll cycle (Demmig-Adams *et al.* 1996) as highlighted by a higher Car content (*i.e*. lower Chl/Car) and by the maintenance of the electron flux involved in alternative pathways such as photorespiration (Asada 1999, Ort and Baker 2002). This is attested by the more than 100% higher P_r and a lower ETR_A/ETR_P ratio in sun.

The multiple regression analysis confirmed the above results selecting ETR_A/ETR_P, Φ_{PSII}, N_a, and Chl (*a*+*b*) as the most significant variables explaining P_N variations in sun and Chl *a*/*b* in shade.

Plant physiological and morphological plasticity contribute to adaption to light environments that species inhabit (Walters and Reich 1996) and a high phenotypic plasticity may increase tolerance to varying environmental conditions and lead to a higher fitness (Sultan 1995). The high PI (0.33) attests *C. avellana* responsiveness to light variations. In particular, the greater plasticity of morphological leaf traits (PI_m = 0.41) than of physiological (PI_p = 0.36) and anatomical (PI_a = 0.24) ones attests to the shade tolerance of *C. avellana* (Yamashita *et al*. 2000, Valladares *et al.* 2002, 2005; Catoni *et al*. 2012). On the whole, the results highlight the ability of *C. avellana* sun plants to prevent photoinhibition of photosynthesis under high PPFD by a higher Car content and P_r and lower F_v/F_m, Φ_{PSII}, confirming the *C. avellana* capacity to perform well in sun. *C. avellana* shade tolerance is attested by several adaptations at leaf level which contribute to maximizing understory light capture, reducing carbon loss by respiration, and maintaining positive carbon balance.

References

Ackerly D.D., Dudley S.A., Sultan S.E. *et al.*: The evolution of plant ecophysiological traits: recent advances and future directions. – BioScience **50**: 979-995, 2000.

Adiloglu A., Adiloglu S.: An investigation on nutritional status of hazelnut (*Corylus avellana* L.) grown in acid soils of Turkey. – Arch. Agron. Soil Sci. **50**: 617-622, 2004.

Amthor J.S.: The McCree-de Wit-Penning de Vries Thornley respiration paradigms: 30 years later. – Ann. Bot-London **86**: 1-20, 2000.

Asada K.: The water-water cycle in chloroplasts: Scavenging of active oxygens and dissipation of excess photons. – Annu. Rev. Plant Phys. **50**: 601-639, 1999.

Atkin O.K., Evans J.R., Ball M.C., Siebke K.: Relationships between the inhibition of leaf respiration by light and enhancement of leaf dark respiration following light treatment. – Aust. J. Plant Physiol. **25**: 437-443, 1998.

Bassil N.V., Botta R., Mehlenbacher S.A.: Microsatellite markers in hazelnut: isolation, characterization, and cross-species amplification. – J. Am. Soc. Hortic. Sci. **130**: 543-549, 2005.

Bailey S., Horton P., Walters R.G.: Acclimation of *Arabidopsis thaliana* to the light environment: the relationship between photosynthetic function and chloroplast composition. – Planta **218**: 793-802, 2004.

Bernacchi C.J., Portis A.R., Nakano H. *et al.*: Temperature response of mesophyll conductance. Implications for the determination of rubisco enzyme kinetics and for limitations to photosynthesis in vivo. – Plant Physiol. **130**: 1992-1998, 2002.

Björkman O., Demmig B.: Photon yield of O_2 evolution and chlorophyll fluorescence at 77k among vascular plants free-air carbon dioxide enrichment affect photochemical of diverse origins. – Planta **170**: 489-504, 1987.

Björkman O., Demmig-Adams B.: Regulation of photosynthetic light energy capture, conversion, and dissipation in leaves of higher plants. – In: Schulze E.D., Caldwell M.M. (ed.): Ecophysiology of Photosynthesis. Pp 17-47. Springer-Verlag, Berlin 1994.

Boccacci P., Botta R., Rovira M.: Genetic diversity of hazelnut (*Corylus avellana* L.) germplasm in northeastern Spain. – HortScience **43**: 667-672, 2008.

Cai Z.Q., Slot M., Fan Z.X.: Leaf development and photosynthetic properties of three tropical tree species with delayed greening. – Photosynthetica **43**: 91-98, 2005.

Castagneri D., Garbarino M., Nola P.: Host preference and growth patterns of ivy (*Hedera helix* L.) in a temperate alluvial forest. – Plant Ecol. **214**: 1-9, 2013.

Catoni R., Gratani L., Varone L.: Physiological, morphological and anatomical trait variations between winter and summer leaves of *Cistus* species. – Flora **207**: 442-449, 2012.

Chabot B.F., Chabot J.F.: Effects of light and temperature on leaf anatomy and photosynthesis in *Fragaria vesca*. – Oecologia **26**: 363-377, 1977.

de Lucia E.H., Whitehead D., Clearwater M.J.: The relative limitation of photosynthesis by mesophyll conductance in co-occurring species in a temperate rainforest dominated by the conifer *Dacrydium cupressinum*. – Funct. Plant Biol. **30**:1197-1204, 2003.

Demmig-Adams B., Adams W.W.III.: Xanthophyll cycle and light stress in nature: Uniform response to excess direct sunlight among higher plants species. – Planta **198**: 460-470, 1996.

Demmig-Adams B., Adams W.W. III, Barker D.H. *et al.*: Using chlorophyll fluorescence to assess the fraction of absorbed light allocated to thermal dissipation of excess excitation. – Physiol. Plantarum **98**: 253-264, 1996.

Dorn L.A., Pyle E.H., Schmitt J.: Plasticity to light cues and resources in *Arabidopsis thaliana*: testing for adaptive value and costs. – Evolution **54**: 1982-1994, 2000.

Duan B., Lü Y., Yin C., Li C.: Morphological and physiological plasticity of woody plant in response to high light and low light. – Chin. J. Appl. Environ. Biol. **11**: 238-245, 2005.

Epron D., Godard D., Cornic G., Genty B.: Limitations of net CO_2 assimilation rate by internal reistances to CO, transfer in leaves of two tree species (*Fagus sylvatica* L. and *Castanea sativa* Mill.). – Plant Cell Environ. **18**: 43-51, 1995.

Evans J.R., Poorter H.: Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. – Plant Cell Environ. **24**: 755-767, 2001.

FAO Production Yearbook: http://faostat.fao.org/site/339/default.aspx. 2011.

FAOSTAT: Food and Agricultural Organization of the United Nations. Production, Crops. http://faostat.fao.org/site/567/default.aspx#ancor. 2012.

FAOSTAT: Agriculture Data. http://faostat3.fao.org/home/index.html. 2013.

Genty B., Briantais J.M., Baker N.R.: The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. – Biochim. Biophys. Acta **990**: 87-92, 1989.

Givnish T.J.: Adaptation to sun and shade: A whole plant perspective. – Aust. J. Plant Physiol. **15**: 63-92, 1988.

Grassi G., Magnani F.: Stomatal, mesophyll conductance and biochemical limitations to photosynthesis as affected by drought and leaf ontogeny in ash and oak trees. – Plant Cell Environ. **28**: 834-849, 2005.

Gratani L., Foti I.: Estimating forest structure and shade tolerance of the species in a mixed deciduous broad-leaved forest in Abruzzo, Italy. – Ann. Bot. Fenn. **35**: 75-83, 1998.

Gratani L., Meneghini M., Pesoli P., Crescente M.F.: Structural and functional plasticity of *Quercus ilex* seedlings of different provenances in Italy. – Trees **17**: 515-521, 2003.

Hampson C.R., Azarenko A.N., Potter J.R.: Photosynthetic rate, flowering, and yield component alteration in hazelnut in response to different light environments. – J. Amer. Soc. Hort. Sci. **121**: 1103-1111, 1996.

Harley P.C., Loreto F., di Marco G., Sharkey T.D. :Theoretical consideration when estimating the mesophyll conductance to CO_2 flux by analysis of the response of photosynthesis to CO_2. – Plant Physiol. **98**: 1429-1436, 1992.

Herr-Turoff A., Zedler J.B.: Does morphological plasticity of the *Phalaris arundinacea* canopy increase invasiveness? – Plant Ecol. **193**: 265-277, 2007.

Holm G.: Chlorophyll mutations in barley. – Acta Agr. Scand. **4**: 457-471, 1954.

Huang D., Wu L., Chen J.R., Dong L.: Morphological plasticity, photosynthesis and chlorophyll fluorescence of *Athyrium pachyphlebium* at different shade levels. – Photosynthetica **49**: 611-618, 2011.

Iglesias-Prieto R., Trench R.K.: Acclimation and adaptation to irradiance in symbiotic dino flagellates. II. Response of chlorophyll-protein complexes to different photon-flux densities. – Mar. Biol. **130**: 23-33, 1997.

Johnson G.N., Young A.J., Scholes J.D., Horton P.: The dissipation of excess excitation energy in British plant species. – Plant Cell Environ. **16**: 673- 679, 1993.

Kasapligil B.: A bibliography on *Corylus* (Betulaceae) with annotations. – Annu. Rep. North. Nut. Growers Assoc. **63**:107-162, 1972.

Koike T., Kitao M., Maruyama Y. *et al*.: Leaf morphology and photosynthetic adjustments among deciduous broad-leaved trees within the vertical canopy profile. – Tree Physiol. **21**: 951-958, 2001.

Krall J.P., Edwards G.E.: Relationship between photosystem II activity and CO_2 fixation in leaves. – Physiol. Plantarum **86**: 180-187, 1992.

Kull O., Niinemets Ü.: Variations in leaf morphometry and nitrogen concentration in *Betula pendula* Roth., *Corylus avellana* L. and *Lonicera xylosteum* L. – Tree Physiol. **12**: 311-318, 1993.

Lam E., Oritz W., Mayfield S., Malkin R.: Isolation and characterization of a light-harvesting chlorophyll *a*/*b* protein complex associated with photosystem I. – Plant Physiol. **74**: 650-655, 1984.

Larcher W.: Physiological Plant Ecology. 4th ed. Pp. 514. Springer, Berlin, 2003.

Loveys B.R., Scheurwater I., Pons T.L. *et al*.: Growth temperature influences the underlying components of relative growth rate: an investigation using inherently fast- and slow-growing plant species. – Plant Cell Environ. **25**: 975-988, 2002.

Maclachlan S., Zalik S.: Plastid structure, chlorophyll concentration, and free aminoacid composition of a chlorophyll mutant of barley. – Can. J. Bot. **41**: 1053-1062, 1963.

Matos F.S., Wolfgramm R., Gonçalves F.V. *et al*.: Phenotypic plasticity in response to light in the coffee tree. – Environ. Exp. Bot. **67**: 421-427, 2009.

Matos F.S., de Oliveria L.R., de Freitas R.G. *et al*.: Physiological characterization of leaf senescence of *Jatropha curcas* L. populations. – Biomass Bioenerg. **45**: 57-64, 2012.

Mendes M.M., Gazarini L.C., Rodrigues M.L.: Acclimation of *Myrtus communis* to contrasting Mediterranean light environments–effects on structure and chemical composition of foliage and plant water relations. – Environ. Exp. Bot. **45**: 165-178, 2001.

Moraes G.A.B.K., Chaves A.R.M., Martins S.C.V. *et al*.: Why is it better to produce coffee seedlings in full sunlight than in the shade? A morphophysiological approach. – Photosynthetica **48**: 199-207, 2010.

Motta R., Nola P., Berretti R.: The rise and fall of the black locust (*Robinia pseudoacacia* L.) in the "Siro Negri" Forest Reserve (Lombardy, Italy): lessons learned and future uncertainties. – Ann. For. Sci. **66**: 410-419, 2009.

Navas M.L., Garnier E.: Plasticity of whole plant and leaf traits in *Rubia peregrina* in response to light, nutrient and water availability. – Acta Oecol. **23**: 375-383, 2002.

Niinemets Ü.: Role of foliar nitrogen in light harvesting and shade tolerance of four temperate deciduous woody species. – Funct. Ecol. **11**: 518-531, 1997.

Niinemets Ü., Kull O., Tenhunen J.D.: An analysis of light effects on foliar morphology, physiology, and light interception in temperate deciduous woody species of contrasting shade tolerance. – Tree Physiol. **18**: 681-696, 1998.

Niinemets Ü., Valladares F.: Photosynthetic acclimation to simultaneous and interacting environmental stresses along natural light gradients: optimality and constraints. – Plant Biol. **6**: 254-268, 2004.

Ort D.R., Baker N.R.: A photoprotective role for O_2 as an alternative electronic sink in photosynthesis? – Curr. Opin. Plant Biol. **5**:193-98, 2002.

Pearcy R.W., Sims D.A.: Photosynthetic acclimation to changing light environments: scaling from the leaf to the whole plant. – In: Roy J., Caldwell M.M., Pearcy R.W. (ed.): Exploitation of Environmental Heterogeneity by Plants. Ecophysiological Processes Above- and Belowground. Physiological Ecology. Pp. 145–174. Academic Press, San Diego 1994.

Percerisa J., Rafecas M., Castellote A.I. *et al*. : Influence of variety and geographical origin on the lipid fraction of halzenuts (*Corylus avellana* L.) from Spain: III. Oil stability, tocopherol content and some mineral contents. – Food Chem. **53**: 71-74, 1995.

Pershern A.S., Breene W.M., Lulai E.C.: Analysis of factors influencing lipid oxidation in hazelnuts (*Corylus* sp.). – J. Food Process. Pres. **19**: 9-26, 1995.

Persson H., Widén B., Andersson S., Svensson L.: Allozyme diversity and genetic structure of marginal and central populations of *Corylus avellana* L. (Betulaceae) in Europe. – Plant Syst. Evol. **244**: 157-179, 2004.

Pignatti S.: [Flora of Italy.] Vol. 1, Pp. 112. Bologna Edagricole, 1982. [In Italian]

Pintado A., Valladares F., Sancho L.G.: Exploring phenotypic plasticity in the lichen *Ramalina capitata* : morphology, water relations and chlorophyll content in north- and south-facing populations. – Ann. Bot.-London **80**: 345-353, 1997.

Poorter L., Kwant R., Hernández R. *et al*.: Leaf optical properties in Venezuelan cloud forest trees. – Tree Physiol. **20**: 519-526, 2000.

Reich P.B., Kloeppel B.D., Ellsworth D.S., Walters M.B.: Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. – Oecologia **104**: 24-30, 1995.

Sack L., Melcher P.J., Liu W.H. *et al*.: How strong is intra-canopy leaf plasticity in temperate deciduous trees? – Am. J. Bot. **93**: 829-839, 2006.

Sartori F.: [Alluvial forests of the lower Ticino valley (Northern Italy)]. – Colloq. Phytosiol. **9**: 201-216, 1984. [In French].

Schlichting C.D.: The evolution of phenotypic plasticity in plants. – Annu. Rev. Ecol. Syst. **17**: 667-693, 1986.

Schulze E.D., Küppers M.: Short-term and long-term effects of plant water deficits on stomatal response to humidity in *Corylus avellana* L. – Planta **146**: 319-326, 1979.

Shahidi F., Alasalvar C., Liyana-Pathirana C.M.: Antioxidant phytochemicals in hazelnut kernel (*Corylus avellana* L.) and hazelnut byproducts. – J. Agric. Food Chem. **55**: 1212-1220, 2007.

Sims J.R., Haby V.A.: Simplified colorimetric determination of soil organic matter. – Soil Sci. **112**: 137-141,1971.

Soolanayakanahally R.Y., Guy R.D., Silim S.N. *et al*.: Enhanced assimilation rate and water use efficiency with latitude through increased photosynthetic capacity and internal conductance in balsam poplar (*Populus balsamifera* L.). – Plant Cell Environ. **32**: 1821-1832, 2009.

Sultan S.E.: Phenotypic plasticity and plant adaptation. – Acta Bot. Neerl. **44**: 363-383, 1995.

Sultan S.E.: Phenotypic plasticity for plant development, function and life history. – Trends Plant Sci. **5**: 537-542, 2000.

Thiele A., Krause G.H., Winter K.: In situ study of photoinhibition of photosynthesis and xanthophyll cycle activity in plants growing in natural gaps of the tropical forest. – Aust. J. Plant Physiol. **25**: 189-195, 1998.

Valentini R., Epron D., de Angelis P. *et al*.: *In situ* estimation of net CO_2 assimilation, photosynthetic electron flow and photorespiration in Turkey oak (*Q. cerris* L.) leaves: diurnal cycles under different levels of water supply. – Plant Cell Environ. **18**: 631-640, 1995.

Valentini N., Calizzano F., Boccacci P., Botta R.: Investigation on clonal variants within the hazelnut (*Corylus avellana* L.) cultivar 'Tonda Gentile delle Langhe'. − Sci. Hortic.-Amsterdam **165**: 303-310, 2014.

Valladares F., Wright S.J., Lasso E. *et al*.: Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. – Ecology **81**: 1925-1936, 2000.

Valladares F., Chico J.M., Aranda I. *et al*.: The greater seedling high-light tolerance of *Quercus robur* over *Fagus sylvatica* is linked to a greater physiological plasticity. – Trees **16**: 395-403, 2002.

Valladares F., Arrieta S., Aranda I. *et al*.: Shade tolerance, photoinhibition sensitivity and phenotypic plasticity of *Ilex aquifolium* in continental-Mediterranean sites. – Tree Physiol. **25**: 1041-1052, 2005.

Violante P.: [Chemical Methods of Soil Analysis.] Pp. 60. Franco Angeli Editore, Milan 2000. [In Italian]

Walters M.B., Reich P.B.: Are shade tolerance, survival, and growth linked? Light and nitrogen effects on hardwood seedlings. – Ecology **77**: 841-853, 1996.

Walters M.B., Reich P.B.: Low-light carbon balance and shade tolerance in the seedlings of woody plants: do winter deciduous and broad-leaved evergreen species differ? – New Phytol. **143**: 143-154, 1999.

Whitcher I.N., Wen J.: Phylogeny and biogeography of *Corylus* (Betulaceae): inference from ITS sequences. – Syst. Bot. **26**: 283-298, 2001.

Yamashita N., Ishida A., Kushima H., Tanaka N.: Acclimation to sudden increase in light favouring an invasive over native trees in subtropical islands, Japan. – Oecologia **125**: 412-419, 2000.

Zunzunegui M., Ain-Lhout F., Díaz Barradas M.C. *et al*.: Physiological, morphological and allocation plasticity of a semi-deciduous shrub. – Acta Oecol. **35**: 370-379, 2009.

Zunzunegui M., Díaz Barradas M.C., Ain-Lhout F. *et al*.: Seasonal physiological plasticity and recovery capacity after summer stress in Mediterranean scrub communities. – Plant Ecol. **212**: 127-142, 2011.