PHOTOSYNTHETICA 43 (4): 615-619, 2005

BRIEF COMMUNICATION

Photosynthetic response of *Quercus ilex* L. plants grown on compost and exposed to increasing photon flux densities and elevated CO_2

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Abstract

Quercus ilex plants grown on two different substrates, sand soil (C) and compost (CG), were exposed to photosynthetic photon flux densities (PPFD) at 390 and 800 μmol(CO_2) mol^{-1} (C_{390} and C_{800}). At C_{800} both C and CG plants showed a significant increase of net photosynthetic rate (P_N) and electron transport rate (ETR) in response to PPFD increase as compared to C_{390}. In addition, at C_{800} lower non-photochemical quenching (NPQ) values were observed. The differences between C_{390} and C_{800} were related to PPFD. The higher P_N and ETR and the lower dissipative processes found in CG plants at both CO_2 concentrations as compared to C plants suggest that substrate influences significantly photosynthetic response of *Q. ilex* plants. Moreover, short-term exposures at elevated CO_2 decreased nitrate photo-assimilation in leaves independently from substrate of growth.

Additional key words: chlorophyll fluorescence induction; electron transport rate; irradiance; nitrate; oak; non-photochemical quenching.

The quality of growth substrate and in particular the nutrient content influences plant growth, photosynthetic capacity, and processes linked to the absorbed photon energy (Makino *et al.* 1992, Godde and Hefer 1994, Lawlor 1995, Joel *et al.* 1997). Several studies demonstrate that ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) and protein contents, CO_2 assimilation, and maximal photochemical PS2 efficiency are strongly influenced by nitrogen availability (Lu and Zhang 2000, Da Matta *et al.* 2002, Lawlor 2002). Moreover, nutrients, in particular nitrate supply to the soil, often increase electron transport rate (ETR) either at low or at high photosynthetic photon flux density (PPFD) (Mourcuende *et al.* 1998, Bloom *et al.* 2002) highlighting the contribute of nitrate assimilation to sustain the electron flow at different PPFD.

An important aspect related to fertilization is the positive photosynthetic response to elevated CO_2 (EC) when plants are grown on a substrate rich in nutrients. The exposure of well fertilized plants to EC can lead to an increase of carboxylation efficiency of RuBPCO (Liu *et al.* 2002). When N supply is limiting, the exposure to EC does not positively affect the plants and down-regulation of photosynthesis occurs (Nakano *et al.* 1997, Rogers *et al.* 1996, 1998).

Compost is good quality manure for agricultural purposes because of improvements of chemical and physical soil properties (Ouédraogo *et al.* 2001). Differently from a customary fertilizer, it is a source and reserve of many nutrients required by plants and releases all inorganic

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Received 7 March 2005, *accepted* 7 June 2005.

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Abbreviations: AQ_F – ratio of net CO_2 assimilation to gross rate of O_2 evolution from chlorophyll fluorescence; C – control plants; C_i/C_a – ratio of intercellular to ambient CO_2 concentration; CEC – cation exchange capacity; CG – compost grown plants; Chl – chlorophyll; EC – elevated CO_2 concentration; ETR – electron transport rate; ETR_{O2} – the gross rate of O_2 evolution from chlorophyll fluorescence; F_0 – background fluorescence; F_m' – maximal fluorescence of closed PS2 reaction centres in the light-adapted state; F_m – maximal fluorescence of closed PS2 reaction centres in the dark-adapted state; F_t – steady-state fluorescence signal in the light-adapted state; F_v/F_m – maximum photochemical efficiency of PS2; NPQ – non-photochemical quenching; N-NO_3^- – nitrate content; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; PS2 – photosystem 2; RuBPCO – ribulose-1,5-bisphosphate carboxylase/oxygenase; Φ_{PS2} – quantum yield of electron transport.

Acknowledgements: The research was supported by a grant from Project of Campania region (legge 5, annualità 2002). The authors acknowledge the Corpo Forestale dello Stato of Sabaudia (Latina, Italy) for providing the plants used for the experiments. The authors are grateful to Dr. Giulia Maisto, Dr. Rosaria D'Ascoli, and Dr. Rossana Marzaioli for support in soil analyses.

elements gradually during its decomposition (Garcia *et al*. 1992, Schelegel 1992). In this work we tested the photosynthetic performance of *Quercus ilex* L. plants grown on compost and exposed to increasing PPFD at 390 and 800 µmol(CO_2) mol^{-1} (C_{390}, C_{800}) to evaluate the simultaneous effects of soil and air fertilization. In particular, the research was focused on the partitioning of absorbed radiation energy between assimilative and dissipative processes at irradiances lower and higher than those needed for photosynthetic saturation.

Two-year-old plants of *Quercus ilex* L. were divided in two groups: the first was planted in pots filled with sand soil (control, C), the second was planted in pots filled with a mixture of compost and expanded clay (CG), of 65 and 35 % of fresh mass, respectively. The compost originated from urban vegetable- and organic-wastes. The plants were grown outdoors, in the Department of Plant Biology of Naples University, in February 2004 and measurements were performed in May and June 2004. No additional nutritive solution was supplied to plants. Fully expanded leaves of new generation at the same developmental stage (about 30 d) were selected for the gas exchange and chlorophyll (Chl) fluorescence measurements.

Gas exchanges parameters were measured by a portable gas exchange system (*HCM-1000*, *Walz*, Effeltrich, Germany) on fully expanded leaves of *Q. ilex* at PPFD from 50 to 1 600 µmol(photon) m^{-2} s^{-1} at C_{390} and C_{800}. The different PPFD on the leaf surface was obtained by a halogen lamp (*1050-H*, *Walz*) positioned on the cuvette plane of *HCM-1000*; the different CO_2 concentrations were obtained by a gas mixing unit (*GMA-4*, *Walz*). All gas exchange parameters were calculated by the software operating in *HCM-1000* according to Caemmerer and Farquhar (1981).

Chl fluorescence emission was measured simultaneously to gas exchange by a portable pulse amplitude modulated fluorometer (*MINI-PAM*, *Walz*) equipped with a 2-mm diameter fibre optics inserted at 60° angle at the leaf plane in the cuvette lid of the gas exchange system. Measuring radiation of about 0.5 µmol(photon) m^{-2} s^{-1} was set at frequency of 600 Hz to obtain, on 30 min dark-adapted sample, background fluorescence signal (F_0). Maximal fluorescence (F_m) was obtained by imposing to the leaf a 1 s saturating flash of about 10 000 µmol(photon) m^{-2} s^{-1}. F_0 and F_m were used to calculate the maximum photochemical efficiency of PS2 [$F_v/F_m = (F_m - F_0)/F_m$]. Under each PPFD, to measure the steady-state fluorescence signal (F_t), the frequency was shifted to 20 kHz. Maximal fluorescence in the light (F_m’) was obtained, at the same frequency, by imposing to the leaf a 1 s saturating flash of about 10 000 µmol(photon) m^{-2} s^{-1}. The quantum yield of PS2 linear electron transport (Φ_{PS2}) was calculated as $\Phi_{PS2} = (F_m' - F')/F_m'$ according to Genty *et al.* (1989) and used for the calculation of linear ETR according to Krall and Edwards (1992): ETR = Φ_{PS2}×PPFD×0.84×0.5, where PPFD represents the photon flux density incident on the leaf, 0.84 is the assumed leaf absorbance, and 0.5 is a factor that implicates equal distribution of energy between photosystems (Krall and Edwards 1992). Stern-Volmer non-photochemical quenching (NPQ) was expressed according to Bilger and Björkman (1990): NPQ = $(F_m - F_m')/F_m'$.

The assimilatory quotient AQ_F calculated as ratio of net photosynthetic rate (P_N) to the gross rate of O_2 evolution (ETR_{O2}) from Chl fluorescence, was used as a measure of foliar NO_3^- assimilation (Searles and Bloom 2003). ETR_{O2} was calculated as ETR/4 according to Edwards and Baker (1993).

After 95 d from planting on substrates C and CG, branches with 30-d-old leaves were cut in the water and then used for measurements in laboratory. Each leaf was initially darkened for 30 min to determine F_v/F_m and then exposed to different PPFD. P_N was determined both at C_{390} and C_{800} by exposing leaves progressively to increasing PPFD from 50 to 1 600 µmol(photon) m^{-2} s^{-1}. During the measurements the leaf temperature was maintained at 25±1.3 °C and relative humidity was 65 %. At each PPFD, when the P_N steady state was reached, P_N was monitored and a saturating light pulse was applied in order to measure the fluorescence parameters Φ_{PS2}, ETR, and NPQ. The steady-state P_N at each PPFD was reached after 40 min. Gas exchange and Chl fluorescence measurements were performed in five replicates.

Organic matter and CEC were determined according to Allen (1974) and Ministero delle Risorse Agricole e Forestali (1994), respectively, whereas nitrate content was determined colorimetrically by *LCK 340* spectrophotometer (*Lange*, Düsseldorf, Germany). Statistical analyses were performed by one-way ANOVA followed by Student-Newman-Keuls test (*Sigma-Stat 1.0*).

P_N measured at C_{800} was significantly ($p<0.001$) higher than that at C_{390} in the whole range of PPFD, independently of growth substrates (Fig. 1*A*). Moreover, at C_{390} P_N saturation was reached near 800 µmol(photon) m^{-2} s^{-1}, while at C_{800} it was reached near 1 000 µmol(photon) m^{-2} s^{-1}. P_N of CG leaves, measured at both CO_2 concentrations, was significantly higher ($p<0.01$) than that of C leaves (Fig. 1*A*).

The exposure at C_{800} determined, starting from 600 µmol(photon) m^{-2} s^{-1}, a significant ($p<0.001$) ETR increase as compared to C_{390} for both CG and C leaves. This increase was higher ($p<0.01$) in CG as compared to C leaves (Fig. 1*B*).

ETR, measured at C_{390}, reached the saturation at 1 000 µmol(photon) m^{-2} s^{-1}, while at C_{800} the ETR saturation was found at 1 200 µmol(photon) m^{-2} s^{-1}. The exposure to C_{800} as compared to C_{390}, in the whole PPFD range, lead to higher ($p<0.05$) AQ_F values whereas no statistical differences between C and CG leaves were detected at both CO_2 concentrations (Fig. 1*C*). Moreover, the increase of PPFD lead to a reduction of AQ_F values both in C and CG leaves.

At increasing irradiances a significant ($p<0.05$) NPQ rise was observed, either at C_{390} or C_{800} in both C and CG leaves. However, at C_{800}, less photon energy was thermally dissipated ($p<0.01$) as compared to C_{390} in both C and CG leaves (Fig. 1*D*). Significant differences ($p<0.01$) were evidenced also between C and CG leaves; in particular the NPQ of CG leaves was always lower than in C leaves at high PPFD. Soil analyses showed higher contents of O_3^- and organic matter, and cation exchange capacity (CEC) in CG as compared to C soil (Table 1).

Table 1. Contents of organic matter and nitrate, and cation exchange capacity (CEC) in sand soil and compost. Means of 3 replicates ± standard errors. Different letters indicate statistically significant differences between substrates.

Substrate	Organic matter [%(d.m.)]	Nitrate content [g kg^{-1}]	CEC [cmol(+) kg^{-1}]
Sand soil	6.1 ± 0.18 ^{a}	0.04 ± 0.005 ^{a}	27.52 ± 0.29 ^{a}
Compost	30.4 ± 1.24 ^{b}	122.00 ± 5.400 ^{b}	51.13 ± 1.21 ^{b}

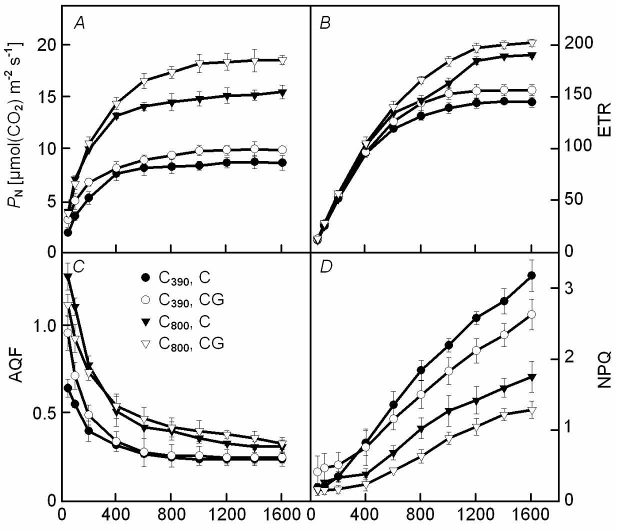

Fig. 1. Effects of different photon flux densities (PPFD) on net photosynthetic rate, P_N (*A*), electron transport rate, ETR (*B*), assimilatory quotient, AQ_F (*C*), and thermal dissipation expressed by non-photochemical quenching, NPQ (*D*) in *Quercus ilex* plants grown on sand soil (C) and compost (CG) measured at 390 and 800 µmol mol^{-1} CO_2 concentration (C_{390}, C_{800}). Measurements were carried out at 25 °C and 65 % relative humidity. Means ± standard error of five measurements.

In C_3 plants a short-term exposure to double CO_2 concentration increases P_N by 50 % or more (Wu *et al.* 1997, Griffin *et al.* 2000). In our study P_N increased by 74 % in C leaves and by 84 % in CG ones under C_{800} at high PPFD (Fig. 1*A*). EC increases P_N and decreases photorespiration due to the characteristics of RuBPCO (Wu *et al.* 1997, Griffin *et al.* 2000). However, the response to C_{800} was due not only to photorespiration reduction at EC, but also to a significant increase of carboxylation efficiency, measured as the ratio of intercellular to ambient CO_2 concentration, C_i/C_a (data not shown). Carbon fixation by RuBPCO is more efficient at EC than at normal CO_2 concentration (Sage 1990). Since photosynthetic activity is often limited by nutrient availability (Wykoff *et al.* 1998, Lima *et al.* 1999), the higher photosynthetic capacity in CG leaves as compared to C leaves could be attributed to nutrient's richness in the compost. The higher ETR ($p<0.001$) together with the higher P_N at C_{800} in both C and CG leaves at PPFD>600 µmol(photon) m^{-2} s^{-1} (Fig. 1*B*) indicated that, at non-limiting PPFD, PS2 linear electron flow was engaged mainly to carbon fixation (Hogan *et al.* 1997, Griffin *et al.* 2000). In addition, the ETR values significantly higher ($p<0.01$) in CG leaves than C leaves, at both CO_2 concentrations, indicated that the growth of *Q. ilex* on compost had a positive effect on ETR as compared to growth on C soil. This is consistent with the observation that in C_3 plants receiving an adequate nutrient supply, ETR often increases (De la Torre *et al.* 1991, Bloom *et al.* 2002). These increases tend to be light-dependent with the greatest differences found at high PPFD.

Assimilation of nitrate and CO_2 may compete for reductant such as ferredoxin of electron transport chain (Bloom *et al.* 2002). AQ_F, *i.e.* ETR/4 according to Edwards and Baker (1993), is an index to evaluate the nitrate photo-assimilation in leaves. Searles and Bloom (2003) suggested that nitrate photo-assimilation in leaves leads to an ETR_{O2} increase whereas P_N can diminish or remain unchanged. Consequently, low AQ_F values indicate a high nitrate photo-assimilation in leaves. In *Q. ilex* leaves, at both C_{390} and C_{800}, the nitrate photo-assimilation increased with increasing PPFD but was not influenced by the growth on different substrates (Fig. 1*C*). In contrast, AQ_F was influenced significantly by exposure to diverse CO_2 concentrations. The exposure to C_{800} decreased nitrate photo-assimilation in leaves. This result is in contrast with findings of Matt *et al.* (2001) that at EC, diminished rates of photorespiration may allow for more photosynthetic energy to be used in foliar nitrate assimilation. On the contrary, we observed, in agreement with results of Searles and Bloom (2003) on *Lycopersicon esculentum*, a higher NO_3^- photo-assimilation in *Q. ilex* leaves at C_{390} than C_{800}. A possible explanation may be linked to the higher photorespiratory activity at atmospheric CO_2 concentration than at EC. Photorespiration increases cytosolic NADH/NAD ratio *via* the export of malate from the chloroplast (Backhausen *et al.* 1994) and high concentration of NADH in the cytosol is essential for the first step of NO_3^- assimilation.

Since nitrate photo-assimilation induces an increase of electron transport and a reduction or no changes in photosynthetic activity, we suggest that increase of photosynthetic electron transport in CG compared to C leaves is not attributable to higher leaf nitrate photo-assimilation, notwithstanding the higher N-NO_3^- content in compost. ETR increase may be due to higher demand for reductive power by CO_2 assimilation. We ascribed the higher photosynthetic activity in CG leaves to the quality of the growth substrate as the compost showed not only a higher N-NO_3^- content, but also a higher organic matter content and CEC as compared to control soil (Table 1).

Different CO_2 concentrations and PPFD have influenced significantly the thermal dissipation in *Q. ilex* plants. The proportion of absorbed photons that is thermally dissipated often gets a maximum before saturating irradiances are reached (Muller *et al*. 2001). We found a rise ($p<0.05$) in NPQ at both CO_2 concentrations and growth conditions with the highest value at 1 600 μmol(photon) m^{-2} s^{-1} (Fig. 1*D*). This result suggests that when photosynthetic activity reaches the saturation, the thermal dissipation becomes an important safety valve for the excess of excitation energy at irradiance higher than the saturation one.

The lower NPQ at C_{800} in both C and CG leaves in the PPFD range of 600–1 600 μmol(photon) m^{-2} s^{-1} (Fig. 1*D*) are consistent with the higher P_N and ETR values of leaves in EC atmosphere. When the absorbed photon energy is used mainly for carbon assimilation, the safety process (thermal dissipation) decreases. Moreover, the differences in NPQ values between C and CG leaves suggest besides the influence of CO_2 also that of growth conditions in reducing thermal dissipation processes. We think that compost, providing an adequate nutrients supply for growth of *Q. ilex* plants, promotes higher photon energy utilization in carbon assimilation rather than in dissipative processes. We hypothesize that the highest NPQ found in C leaves grown on a low nutrient substrate may be attributed to an increase in antheraxanthin and zeaxanthin correlated with thermal dissipation (Demmig-Adams *et al*. 1996, Horton *et al.* 1996). Plants grown under limiting nutrient conditions, in particular N, and exposed to high irradiances, show an increase of zeaxanthin and antheraxanthin contents as well as of thermal dissipation (Lu and Zhang 2000, Dong *et al.* 2002, Cheng 2003).

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