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Canopy profiles of photosynthetic parameters under elevated CO_2 and N fertilization in a poplar plantation

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Photosynthetic acclimation occurred only marginally.

Abstract

A poplar plantation has been exposed to an elevated CO_2 concentration for 5 years using the free air CO_2 enrichment (FACE) technique. Even after such a long period of exposure, leaves of *Populus x euramericana* have not shown clear signs of photosynthetic acclimation. Only at the end of the growing season for shade leaves was a decrease of maximum velocity of carboxylation (V_{cmax}) observed. Maximum electron transport rate (J_{max}) was increased by FACE treatment in July. Assimilation rates at CO_2 partial pressure of 400 (A_{400}) and 600 (A_{600}) μmol mol^{-1} were not significantly different under FACE treatment. Most notably FACE significantly decreased stomatal conductance (g_s) both on upper and lower canopy leaves. N fertilization increased N content in the leaves on mass basis (N_m) and specific leaf area (SLA) in both CO_2 treatments but did not influence the photosynthetic parameters. These data show that in poplar plantations the long-term effects of elevated CO_2 on photosynthesis do not differ considerably from the short-term ones even with N deposition.

Keywords: FACE; *Populus*; Elevated CO_2; Photosynthesis; Nitrogen

1. Introduction

A stimulation of photosynthetic rate under elevated CO_2 is shown in most of the recent reviews (Gielen and Ceulemans, 2001; Norby et al., 1999; Saxe et al., 1998). However increased photosynthesis may not be sustained over a long-term period under CO_2 enrichment and a down-regulation often occurs after some time. This is especially true for plants growing under limiting conditions which do not allow a maintenance of active sinks necessary to accumulate the surplus of carbohydrates produced under elevated CO_2 (Stitt, 1991). The accumulation of carbohydrates in the leaves due to an

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Abbreviations: A_{400}, rate of CO_2 uptake at CO_2 partial pressure of 400 μmol mol^{-1}; A_{600}, rate of CO_2 uptake at CO_2 partial pressure of 600 μmol mol^{-1}; C_a, CO_2 partial pressure in the air; C_i, CO_2 partial pressure in the leaf; Chl, chlorophyll; E/A, elevated/ambient, i.e. FACE effect expressed as FACE/control; FACE, free air CO_2 enrichment; F/U, fertilised/unfertilised, i.e. fertilization effect; g_s, stomatal conductance; ISF, indirect site factor; J_{max}, maximum rate of electron transport; N_a, leaf nitrogen concentration on leaf area basis; N_m, leaf nitrogen concentration on leaf mass basis; P_i, inorganic phosphate ion; PPFD, photosynthetic photon flux density; RubP, ribulose-1,5-bisphosphate; SLA, specific leaf area; τ, canopy transmittance of PPFD; V_{cmax}, maximum velocity of carboxylation.

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imbalance of source–sink relationships usually induces a feedback mechanism of reduction of photosynthetic capacity (Webber et al., 1994). Sage (1994) proposed that acclimation could occur under elevated CO_2 if the capacity of carboxylation exceeds the capacity to regenerate RubP. Moreover, Harley et al. (1992) suggested that the inorganic phosphate (P_i) required for the RubP regeneration could become limiting under elevated CO_2. Nevertheless, Long and Drake (1992) assessed that there is limited evidence that acclimation of photosynthesis to elevated CO_2 can involve a change in capacity for the regeneration of RubP and suggested that variation in response might be explained by variation in sink strength. Down-regulating responses are usually observed near the end of the growing seasons when the sink strength is dramatically reduced (Sholtis et al., 2004). Moreover, seasonal changes, e.g. low temperature, enhance photosynthetic down-regulation (Tsonev et al., 2003) and the same behaviour is expected with a decline of leaf N (Herrick and Thomas, 2001). Most commonly down-regulation involves a reduction of the maximum velocity of carboxylation (V_{cmax}) and of the maximum electron transport rate (J_{max}). For instance V_{cmax} was 12–20% lower in *Populus deltoides* × *Populus nigra* in mid September, but not in early August (Curtis et al., 1995). The reduction in V_{cmax} under elevated CO_2 has been shown to increase over the course of the season from 9% to 23% (Norby et al., 1999). Down-regulating responses are often due to restrictive experimental conditions such as growth in pots which do not allow a free development of below-ground biomass or growth in chambers which affects the normal development of the aerial portion and/or indirectly modifies the microclimate inducing a well-known chamber effect (Leadley and Drake, 1993). In other cases limitations could originate from modification of processes occurring at the ecosystem level under elevated CO_2 which lead to reduced nutrient availability. A reduction of nitrogen availability during long-term exposure to elevated CO_2 is often observed due to increased removal of N from soil to sustain increased growth rates and/or due to decreased decomposition rates of litter and soil organic matter. Soil N availability usually influences N content in the leaves (Hobbie et al., 2001) which tends itself to be slightly reduced by elevated CO_2. Of course in most cases this reduction can be simply explained as dilution effect, that is as a result of increased accumulation of simple carbohydrates in leaves under elevated CO_2. Nevertheless, species that showed the greatest reductions in leaf N content at elevated CO_2, also showed reduced enhancements in assimilation rates (Nowak et al., 2004). Regardless of this down-regulation, assimilation rates at growth conditions usually remain higher under elevated CO_2 regardless of the duration of the study (Norby et al., 1999).

Leaf position within the canopy can also affect the response of photosynthesis to elevated CO_2. This can be due both to a direct effect, that is the photosynthetic response to elevated CO_2 changes at different light levels, and to an indirect effect since elevated CO_2 can change both microclimatic conditions and leaf properties even when similar crown positions are considered between treatments. Kubiske et al. (1997) observed greater photosynthetic enhancements in elevated CO_2 in the lower half of the crown, although mid-crown leaves exhibited reductions in photosynthetic capacity. It has been hypothesized that elevated CO_2 and shading can interact inducing a stronger acclimation response than either factor alone (DeLucia and Thomas, 2000; Herrick and Thomas, 1999, 2001). For example it has been observed in *Populus tremuloides* that acclimation-response to elevated CO_2 is stronger in shade than in sun leaves (Kubiske et al., 2002).

Acclimation of stomatal conductance under elevated CO_2 may also be crucial to influence assimilation rates; a reduction of about 20% in trees was usually observed (Field et al., 1995) although the responses were very variable depending on the duration of the experiment, the species and the environmental constraints (Saxe et al., 1998). In a meta-analysis by Curtis and Wang (1998), a 10% decrease in stomatal conductance was reported for woody species under elevated CO_2, although this response was not statistically significant.

The possibility to study poplars, which are characterised by unlimited growth, and to perform a CO_2 enrichment using the FACE technique, i.e. in field conditions without environmental constraints and over a long-term period, provides useful information on photosynthetic properties. Moreover, by including the N treatment, it is possible to verify how crucial is the role of this nutrient on the response of fast growing trees to elevated CO_2 over long-term periods. A key question remains, whether acclimation of photosynthesis occurs most prevalently in ecosystems where N is limiting (Nowak et al., 2004). Therefore the objectives of our study were to verify (a) if acclimation occurs in a poplar plantation after 5 years of exposure to elevated CO_2 and how this is influenced by N availability, by light regimes and by the timing within the growing season and (b) if in situ stomatal conductance is reduced under elevated CO_2.

2. Materials and methods

Measurements were carried out at the POPFACE site which is located in Tuscania, Viterbo (central Italy, 42°22′ N, 11°48′ E). Three of the six experimental plots selected within a 9-ha short rotation coppice culture of poplars were maintained at ambient CO_2 (control) whereas the other three were maintained at a CO_2