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Gas exchange acclimation to elevated CO_2 in upper-sunlit and lower-shaded canopy leaves in relation to nitrogen acquisition and partitioning in wheat grown in field chambers

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Abstract

Growth at elevated CO_2 often decreases photosynthetic capacity (acclimation) and leaf N concentrations. Lower-shaded canopy leaves may undergo both CO_2 and shade acclimation. The relationship of acclimatory responses of flag and lower-shaded canopy leaves of wheat (*Triticum aestivum* L.) to the N content, and possible factors affecting N gain and distribution within the plant were investigated in a wheat crop growing in field chambers set at ambient (360 μmol mol^{-1}) and elevated (700 μmol mol^{-1}) CO_2, and with two amounts of N fertilizer (none and 70 kg ha^{-1} applied on 30 April). Photosynthesis, stomatal conductance and transpiration at a common measurement CO_2, chlorophyll and Rubisco levels of upper-sunlit (flag) and lower-shaded canopy leaves were significantly lower in elevated relative to ambient CO_2-grown plants. Both whole shoot N and leaf N per unit area decreased at elevated CO_2, and leaf N declined with canopy position. Acclimatory responses to elevated CO_2 were enhanced in N-deficient plants. With N supply, the acclimatory responses were less pronounced in lower canopy leaves relative to the flag leaf. Additional N did not increase the fraction of shoot N allocated to the flag and penultimate leaves. The decrease in photosynthetic capacity in both upper-sunlit and lower-shaded leaves in elevated CO_2 was associated with a decrease in N contents in above-ground organs and with lower N partitioning to leaves. A single relationship of N per unit leaf area to the transpiration rate accounted for a significant fraction of the variation among sun-lit and shaded leaves, growth CO_2 level and N supply. We conclude that reduced stomatal conductance and transpiration can decrease plant N, leading to acclimation to CO_2 enrichment.

Keywords: *Triticum aestivum* L.; Acclimation; Chlorophyll; Elevated CO_2; Nitrogen; Photosynthesis; Rubisco activity; Stomatal conductance; Transpiration

1. Introduction

A reduction in the photosynthetic capacity of upper-sunlit leaves has often been observed in C_3 plants grown at elevated CO_2 (Drake et al., 1997; Nakano et al., 1997; Rogers and Humphries, 2000; Lee et al., 2001). The loss of photosynthetic capacity in elevated CO_2 has been attributed to a reduction in the amount and activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) (Drake et al., 1997; Rogers and Humphries, 2000), and is more pronounced in conditions where growth may become sink-limited or when plants are grown with a low N supply (Nakano et al., 1997; Rogers et al., 1998), suggesting that N availability plays an important role in maintenance of photosynthetic capacity. Also, the stomatal conductance (g_s) of sunlit leaves is severely reduced in elevated CO_2-grown plants (Drake et al., 1997; Lodge et al., 2001; Medlyn et al., 2001; Tezara et al., 2002). With few exceptions (Osborne et al., 1998; Adam et al., 2000), studies on photosynthetic acclimation to elevated CO_2 have focused on upper-sunlit leaves and little attention has been paid to the acclimatory responses of lower-shaded canopy leaves. In plants growing at elevated CO_2, leaves occupying lower positions will undergo both shade-acclimation, due to the development of upper canopy leaves, and CO_2-acclimation. As a consequence, the photosynthetic acclimation to elevated

Abbreviations: An, photosynthetic carbon assimilation; *E*, transpiration; g_s, stomatal conductance; Rubisco, ribulose-1,5-bisphosphate carboxylase oxygenase

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CO_2 appears to be more pronounced in the lower-shaded and older leaves of the canopy as compared to the uppermost and sunlit leaves (Osborne et al., 1998; Adam et al., 2000). Also, the acclimatory response of g_s to elevated CO_2 could differ among leaves occupying different positions within the canopy.

CO_2 enrichment often leads to decreased N concentration in leaves (Conroy and Hocking, 1993; Stitt and Krapp, 1999) and lower N uptake (Polley et al., 1999) but for reasons that are far from clear. The failure of nitrogen uptake to keep pace with the increased growth rate at elevated CO_2, or dilution of nitrogen by the accumulation of nonstructural carbohydrates (Stitt and Krapp, 1999) cannot provide a satisfactory explanation, particularly when the increases in carbohydrates and dry matter are small. Increased CO_2 leads to decreased stomatal conductance and lower water flow due to transpiration (Stitt and Krapp, 1999). This may decrease the mass flow of water in the soil to the roots and decrease the availability of mobile nutrients such as nitrate (Conroy and Hocking, 1993; Stitt and Krapp, 1999; McDonald et al., 2002), although it has been argued that this will only lead to nitrate becoming limited in low-fertility soils (Stitt and Krapp, 1999), and in any case other factors responding to CO_2 enrichment can compensate for a low, transpiration-limited N supply (McDonald et al., 2002).

Nitrogen nutrition not only increases the amount of nitrogen in the whole canopy but also affects the distribution of N among the different leaves within the canopy, which is more uniform at high N nutrition (Del Pozo, 1994; Dreccer et al., 2000). Accordingly, N nutrition could mitigate CO_2-acclimation, particularly in lower-shaded leaves. Gradients in the leaf N content and photosynthetic capacity within the leaf canopy have been reported for several species (Charles-Edwards et al., 1987; Hirose et al., 1989; Lemaire et al., 1991; Evans, 1993; Lötscher et al., 2003; Yin et al., 2003), including wheat (Del Pozo, 1992; Dreccer et al., 2000). Upper-sunlit leaves usually have higher photosynthetic capacity than shaded ones from lower positions in the canopy, which correlates with the vertical distribution of leaf nitrogen per unit leaf area and with light within the canopy (Del Pozo and Dennett, 1999). It has been found that the difference in the transpiration rate among leaves is an important mediator in the response of plants to the vertical light gradient. Moreover, the allocation of resources to leaves in a canopy responds to the rate of transpiration, regardless of light intensity (Pons et al., 2001).

The aim of this study was to assess the acclimatory responses to elevated CO_2 of gas exchange in flag and lower canopy leaves of wheat growing in the field under ventilated plastic chambers with different levels of N supply, and to analyze the involvement in acclimation of nitrogen accretion and partitioning to above-ground plant parts and the possible relationships between N accumulation and transpiration.

2. Materials and methods

2.1. Site and experimental setup

The experimental site was located at the IRNASA Muñovela Farm at Salamanca (41°N, 800 m.a.s.l.), Spain. The climate in Salamanca corresponds to a Mediterranean type; the long term average of the minimum temperatures of the coldest month (January) is 0.0 °C and of the maximum temperatures

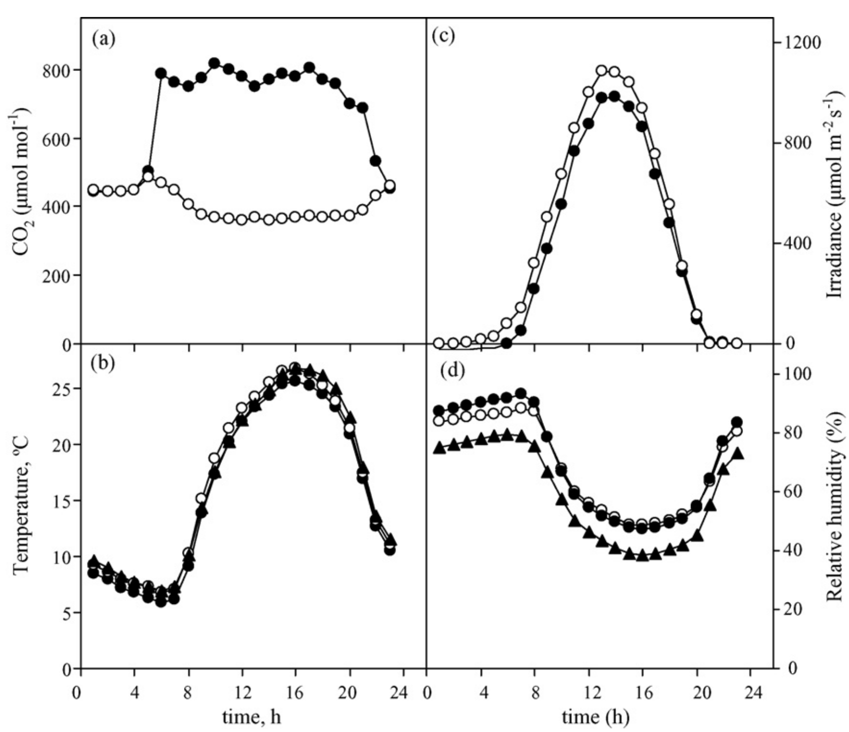

Fig. 1. Mean daily courses of air CO_2 concentration (a), temperature (b), and humidity (d) in field chambers set at either ambient (360 µmol mol^{-1} (◯)) or elevated (700 µmol mol^{-1} (●)) CO_2. The irradiance outside (◯) and inside (●) the chambers is shown in (c) and the temperature and humidity outside the chambers (▲) are shown in (b) and (d).