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Low soil temperature inhibits the effect of high nutrient supply on photosynthetic response to elevated carbon dioxide concentration in white birch seedlings

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Summary To investigate the interactive effects of soil temperature (T_{soil}) and nutrient availability on the response of photosynthesis to elevated atmospheric carbon dioxide concentration ($[\text{CO}_2]$), white birch (*Betula papyrifera* Marsh.) seedlings were exposed to ambient ($360 \mu\text{mol mol}^{-1}$) or elevated ($720 \mu\text{mol mol}^{-1}$) $[\text{CO}_2]$, three T_{soil} (5, 15 and 25 °C initially, increased to 7, 17 and 27 °C, respectively, 1 month later) and three nutrient regimes (4/1.8/3.3, 80/35/66 and 160/70/132 mg l^{-1} N/P/K) for 3 months in environment-controlled greenhouses. Elevated $[\text{CO}_2]$ increased net photosynthetic rate (A_n), instantaneous water-use efficiency (IWUE), internal to ambient carbon dioxide concentration ratio (C_i/C_a), triose phosphate utilization (TPU) and photosynthetic linear electron transport to carboxylation (J_c), and it decreased actual photochemical efficiency of photosystem II ($\Delta F/F_m'$), the fraction of total linear electron transport partitioned to oxygenation (J_o/J_T) and leaf N concentration. The low T_{soil} suppressed A_n , transpiration rate (E), TPU, $\Delta F/F_m'$ and J_c , but it increased J_o/J_T . The low nutrient treatment reduced A_n , IWUE, maximum carboxylation rate of Rubisco, light-saturated electron transport rate, TPU, $\Delta F/F_m'$, J_c and leaf N concentration, but increased C_i/C_a . There were two-factor interactions for C_i/C_a , TPU and leaf N concentration, and a significant effect of $\text{CO}_2 \times T_{\text{soil}} \times$ nutrient regime on A_n , IWUE and J_c . The stimulations of A_n and IWUE by elevated $[\text{CO}_2]$ were limited to seedlings grown under the intermediate and high nutrient regimes at the intermediate and high T_{soil} . For J_c , the $[\text{CO}_2]$ effect was significant only at intermediate T_{soil} + high nutrient availability. No significant $[\text{CO}_2]$ effects were observed under the low T_{soil} at any nutrient level. Our results support this study's hypothesis that low T_{soil} would reduce the positive effect of high nutrient supply on the response of A_n to elevated $[\text{CO}_2]$.

Keywords: *Betula papyrifera* Marsh., boreal forest, CO_2 enrichment, CO_2 - T_{soil} -nutrient interaction, gas exchange, global environmental change.

Introduction

The photosynthetic and growth responses of C_3 plants to elevated carbon dioxide concentration ($[\text{CO}_2]$) show considerable diversity, ranging from highly positive to neutral and, in rare cases, even negative (Poorter 1993, Gunderson and Wullschleger 1994, Miglietta et al. 1996, Zhang and Dang 2007). Such variability in response complicates the prediction of ecosystem changes as CO_2 continues to accumulate in the earth's atmosphere. Plant responses to elevated $[\text{CO}_2]$ are modified by growing conditions (Miglietta et al. 1996, Midgley et al. 1999, Olszyk et al. 2003, Zhang and Dang 2006, Zhang et al. 2006, Cao et al. 2007, Zhang and Dang 2007). For instance, elevated $[\text{CO}_2]$ increases photosynthesis (Davey et al. 1999, Eguchi et al. 2004) and growth (Baxter et al. 1997, Oren et al. 2001) in nutrient-rich but not in nutrient-poor soils. Other environmental factors that are known to influence the responses of C_3 plants to elevated $[\text{CO}_2]$ include soil moisture (Mishra et al. 1999, Robredo et al. 2007), light (Zebian and Reekie 1998, Marfo and Dang 2009) and air temperature (Allen et al. 1990, Pessarakli 2005). However, multiple factors often interact in natural ecosystems to affect plants, and the interactive effects may be of greater value than the main effects in predicting plant responses to elevated atmospheric $[\text{CO}_2]$.

Soil temperature (T_{soil}) is an important environmental factor controlling the growth of northern forests (Bonan and Shugart 1989, Bonan 1992). There is great heterogeneity in T_{soil} among different sites within the boreal forest, ranging from near zero over permafrost to 35 °C on south-facing slopes and newly burnt sites (Bonan and Shugart 1989, Zasada et al. 1997). Low T_{soil} reduces root growth and nutrient uptake (Chapin 1974, Tachibana 1982, Pastor et al. 1987, Pritchard et al. 1990, Paré et al. 1993, Peng and Dang 2003). Plants growing in cold soils may experience feedback inhibition and photoinhibition of photosynthesis because of reduced sink strength (Bagnall et al. 1988, Lambers et al. 2008). Furthermore, low shoot water potentials associated with increased soil water viscosity and decreased root permeability