

CO₂-induced photosynthetic and stoichiometric responses to phosphorus limitation

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Carbon fertilisation from rising atmospheric CO₂ concentrations increases the productivity of plants globally. Meanwhile, the global cycles of Nitrogen (N) and Phosphorus (P) are also altered due to anthropogenic emissions. In general, the additional supply of N is expected to exceed that of P, leading to an increase in P limitation in natural ecosystems. Although the direct carbon fertilisation effect and the interaction with available N is relatively well understood, it remains uncertain how carbon fertilisation is confounded by the availability of P. It is hypothesised that (i) the photosynthetic P-use efficiency increases at elevated CO₂ owing to a direct increase in photosynthesis and (ii) the photosynthetic maximum carboxylation rate (V_{cmax}) and electron transport rate (J_{max}) are down-regulated in response to a combination of elevated CO₂ and P-limitation via a coordinated reduction of leaf N and P content per unit leaf area. In this study we examined the hypothesised effects of P limitation and CO₂ fertilisation on the photosynthetic and stoichiometric responses of three plant species: *Holcus lanatus* (C3 grass), *Panicum miliaceum* (C4 grass) and *Solanum dulcamara* (C3 herb). Individuals of these species were grown at sub-ambient (150 ppm), modern (450 ppm) and elevated CO₂ concentrations (800 ppm) and exposed to an N:P treatment consisting of either severe nitrogen limitation at an N:P ratio of 1:1, or severe P limitation at an N:P ratio of 45:1, with a similar supply rate of N. Our results show significant effects of growth CO₂ and P supply on V_{cmax} and J_{max}, as well as the whole-plant biomass at the point of harvest. Interaction effects between growth CO₂ and P supply were observed for the light-saturated photosynthesis rate, stomatal conductance, leaf P content, and the N:P ratio of the leaf. No significant change in the leaf N content was observed across treatments. These results suggest that limited availability of P constrains the biochemical potential for plants to up-regulate V_{cmax} and J_{max}. This effect is most prominently expressed at low CO₂ growth conditions, which induce strong up-regulation of V_{cmax} and J_{max} when P is not limiting. Conversely, the down-regulation of V_{cmax} and J_{max} at elevated CO₂ is more pronounced when P is limiting. Hence, the combined effects of rising CO₂ and additional P limitation may result in additional down-regulation of V_{cmax} and J_{max} and a subsequent waning of the CO₂ fertilisation effect. These results highlight the need to consider P limitation in global vegetation models when studying carbon fertilisation effects.