

EGU22-1858

<https://doi.org/10.5194/egusphere-egu22-1858>

EGU General Assembly 2022

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## Photosynthetic acclimation under CO<sub>2</sub> fertilization: new perspectives from current experiments

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Photosynthetic acclimation under CO<sub>2</sub> fertilization is still incompletely understood. Observed reductions in the maximum rate of carboxylation ( $V_{\text{cmax}}$ ) and electron transport ( $J_{\text{max}}$ ) under elevated CO<sub>2</sub> (often called 'down-regulation') have been explained in various ways, including limited soil nitrogen (N) and phosphorus (P) availability, or a reduced demand for N. However, there remains large variation of the  $V_{\text{cmax}}$  decline and some non-sensitive or even positive responses are documented. The least cost hypothesis (Prentice et al., 2014) states that optimal photosynthesis is achieved at balanced unit costs of capacities of carboxylation and transpiration and predicts the acclimation of  $V_{\text{cmax}}$  and  $J_{\text{max}}$  in response to the environment. Under elevated CO<sub>2</sub>,  $V_{\text{cmax}}$  is predicted to decline, while the ratio  $J_{\text{max}}/V_{\text{cmax}}$  is predicted to increase - independent of N supply from the soil. In contrast, common model parametrisations conceive  $V_{\text{cmax}}$  to be controlled by soil N supply.

Here, we analyse a compilation of experimental results in an attempt to better understand photosynthetic acclimation to elevated CO<sub>2</sub> and balance the evidence for contrasting model formulations. Within 38 CO<sub>2</sub> fertilization plots investigated at forest, grassland and cropland,  $V_{\text{cmax}}$  and  $J_{\text{max}}$  are shown to decrease in concert, while the ratio  $J_{\text{max}}/V_{\text{cmax}}$  increases with higher CO<sub>2</sub> concentration, consistent with predictions from the least cost hypothesis. However, the predicted increase in the  $J_{\text{max}}/V_{\text{cmax}}$  ratio is too large and the observed change in  $V_{\text{cmax}}$  is correlated with the change in soil inorganic N. Observed leaf N responses are broadly consistent with changes in  $V_{\text{cmax}}$  and  $J_{\text{max}}$ . These findings support the idea acclimation of photosynthetic traits under enhanced CO<sub>2</sub> is modulated by soil N supply. This can be explained by the direct decline of soil N availability at higher CO<sub>2</sub> concentrations. However, it may also be caused by increase rates of net primary production (NPP) and N uptake that increase N sequestered in biomass under elevated CO<sub>2</sub>, in such a way to constrain labile soil N available for leaf-level photosynthesis.

$V_{\text{cmax}}$  and  $J_{\text{max}}$  responses to  $\text{CO}_2$  were also found to be negatively related to increases of above- and below-ground net primary production (ANPP, BNPP). This pattern might be explained by a 'dilution effect', due to a  $\text{CO}_2$ -induced increase of leaf area index (LAI). However, it might also be due to plants having different stomatal responses to  $\text{CO}_2$ . According to this hypothesis, at one end of the spectrum, the ratio of leaf intercellular  $\text{CO}_2$  ( $C_i$ ) relative to ambient  $\text{CO}_2$  ( $C_a$ ) remains constant; optimal photosynthesis increases, while optimal  $V_{\text{cmax}}$  declines. At the other end of the spectrum,  $C_i/C_a$  decreases enough that  $C_i$  remains constant; then there is no increase in optimal photosynthesis, and no change in optimal  $V_{\text{cmax}}$ . Testing this hypothesis would require concomitant measurements of all of the relevant quantities (LAI, NPP,  $C_i/C_a$ ) in multiple experiments.