



## Meta-analysis of the response of crop photosynthesis to nitrogen limitation

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The carbon (C) and nitrogen (N) cycles are intricately linked at all spatial scales. At the smallest, molecular scale, the C and N metabolisms of organisms are interconnected due to the dependence of N acquisition on the C metabolism for the disposal of energy and C skeletons and the dependence of C acquisition on the N metabolism for the provision of proteins and other N compounds. The strong correlation between photosynthetic rate and leaf N content evidences the close relationship between C and N acquisition and represents a central connection between the C and N metabolisms that is used in many regional to global ecosystem models. This small-scale photosynthesis-leaf nitrogen relationship thus translates into the large-scale N control of the terrestrial C cycle.

Despite the importance of N as a major limiting nutrient in terrestrial ecosystems, the general response of photosynthesis and plant growth to N limitation is not yet well understood. Under suboptimal N conditions plants have two possibilities: reducing the leaf N content and the photosynthetic rate or reducing leaf area expansion while maintaining leaf N content relatively constant. So far no consistent picture about the relative importance of different strategies in the response of crops to N limitation has emerged and it thus remains unclear in what detail N limitation needs to be implemented in ecosystem and crop growth models. Is there a general strategy of crops or crop types in dealing with N limitation? To investigate this question, we used the meta-analysis technique to synthesize the literature on the response of 15 different crop species to N limitation. The meta-analysis focused on photosynthetic parameters, including photosynthetic rate, photosynthetic components, leaf N content and leaf area. In addition, the linear photosynthesis - leaf nitrogen relationship of crop species was analyzed in a meta-regression analysis to examine general patterns and differences between crop species and crop types.

Although meta-analysis has been widely used to examine the response of plants to elevated CO<sub>2</sub> concentrations, so far to our knowledge no comprehensive meta-analytic review of plant response to N limitation has been conducted. This study shows that meta-analysis provides a useful tool to draw conclusions from the heterogeneous experimental literature on the effect of N limitation on physiological processes. The meta-analysis shows that crops under limiting N supply decrease the canopy size, accumulate less N, have lower leaf concentrations of proteins and chlorophyll, have a decreased photosynthetic rate, and show increased levels of leaf carbohydrates. Although leaf N content and photosynthetic rate are reduced significantly under N limitation, crop species differ in the extent in which they reduce photosynthesis compared to leaf area. The meta-regression analysis confirms the robustness of the linear relationship between photosynthetic rate and leaf N content for crops. It also shows that there are significant differences in the form of this relationship between crop species with different photosynthetic pathways. The form of the photosynthesis-leaf N relationship is influenced by environmental conditions like the level of CO<sub>2</sub> or the level of N supply and this response differs between crop species. Although thus some general patterns in crop C-N interactions could be observed, the meta-analysis of the N limitation effect as well as the regression analysis of the photosynthesis-leaf N relationship show that crops in general or crop types do not follow a universal strategy in their response to N limitation. Crop species reduce their photosynthetic rate to differing degrees and invest differently in leaf N content and leaf expansion under limiting N supply.