**Grassland plants increase leaf quantity, not leaf quality, in response to soil nitrogen addition**

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**Abstract**

Fossil fuel burning and agricultural runoff are increasing rates of nitrogen inputs to terrestrial ecosystems globally. These inputs may act to alter ecosystem processes and services, including plant productivity. Past studies have shown that nitrogen additions can increase plant productivity; however, the physiological mechanisms underlying this response are not well known. Here, we test use a globally distributed network of grassland nitrogen addition experiments (Nutrient Network) to show that soil nitrogen addition (10 g m-2 yr-1) had no impact on per-leaf-area nitrogen content (*N*area); instead, most (XX%) of the variation in *N*area can be explained by leaf mass per area and climate. Soil nitrogen addition only added XX% explanatory power. However, the soil nitrogen addition significantly increased leaf area index (leaf area per ground area) by 41%. We show that this result can be explained using photosynthetic least-cost theory. That is, plants maximize their leaf and whole plant carbon assimilation at the lowest possible cost. To do this, *N*area is optimized to the climate to maximize carbon assimilation at the lowest nitrogen use. Plants do not increase *N*area under added soil nitrogen because light limitation would result in no change to per-leaf-area photosynthesis. Instead, the added soil nitrogen is used to build new optimized leaf tissue, increase whole plant photosynthesis. These results demonstrate that grassland plants respond to added soil nitrogen by increasing leaf quantity rather than leaf quality.

**Introduction**

Plant processes modulate the impact of global changes on ecosystem processes, including cycling of carbon and nutrients. As such, it is important to understand plant physiological responses to global change to reliably predict future ecosystem processes.

An important future global change is the ongoing increase in terrestrial nitrogen deposition resulting from agricultural expansion and the increase in fossil fuel burning.

Nitrogen limits plant growth in terrestrial ecosystems.

However, competing hypotheses exist for the mechanisms underlying nitrogen fertilization-induced increases in plant growth. One hypothesis suggests that plant photosynthesis is nutrient limited and that an increased availability in soil available nitrogen will stimulate plant uptake and allocation to nutrient demanding photosynthetic enzymes such as Ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco). We term this hypothesis the “photosynthetic nitrogen limitation” hypothesis. Under a scenario where soil nitrogen is increased, this hypothesis would predict that plants would show a strong increase in leaf nitrogen, likely to support Rubisco carboxylation.

The other competing hypothesis posits that an increase in leaf level nitrogen to support carbon assimilation under soil nitrogen addition would be a “wasteful” process in that it would only lead to light limitation of photosynthesis. Instead, this hypothesis suggests that leaf nitrogen is uncoupled from soil nitrogen and instead responds primarily to climate. We term this hypothesis the “least cost” hypothesis. Importantly, this hypothesis only indicates static levels of per-leaf-area nitrogen (and photosynthetic rates) under soil nitrogen addition, but does contradict the commonly observed increases in per plant nitrogen (and photosynthetic rates; or gross primary productivity).

The discrepancy between these two competing hypotheses is not trivial and can have important implications for predictions of future terrestrial carbon cycling.

Here, we use a globally distributed network of nitrogen addition experiments to test these two competing hypotheses.

**Methods**

**Results**

**Discussion**

**Conclusion**