

## RESEARCH ARTICLE

# Facilitation by leguminous shrubs increases along a precipitation gradient

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## Abstract

1. Combining nutrient dynamics (plant nutrient uptake and soil fertility) can help uncover mechanisms of shrub–grass interactions and assess the validity of the stress-gradient hypothesis, which predicts that facilitation between plants increases in stressful environments. However, how facilitation via shrub-mediated nutrient increases varies with precipitation is poorly resolved.
2. We first synthesized a global dataset from 66 studies and evaluated how shrubs affected soil organic carbon (C) and nitrogen (N) in grasslands along a precipitation gradient. We then made new measurements in a single-grassland type encroached by leguminous shrubs from the same genus (*Caragana*) to constrain the variations caused by combining different grassland types and shrubs traits in the meta-analysis. Specifically, we investigated how shrubs mediated N dynamics and how shrub–grass interactions varied along a precipitation gradient (147–342 mm) in a temperate steppe of China.
3. At the global scale, leguminous shrub-mediated effects on soil nutrients increased with precipitation, while no relationship was found for non-leguminous shrub. For the field experiment, greater N and lower  $\delta^{15}\text{N}$  in *Caragana* compared to non-leguminous shrub (reference shrub, *Salsola collina*) suggested active N-fixation in *Caragana*. We found that *Caragana* enhanced N concentration and leaf quality (low C:N ratio) in neighbouring plants more on mesic sites than on xeric sites. Thus, facilitation increased via higher soil N and with decreasing environmental stress, at least along this relatively arid precipitation gradient.
4. Our results highlight the importance of precipitation in determining the nutritional facilitation to neighbouring grasses from encroaching leguminous shrubs. Conceptual frameworks for plant facilitation may therefore need to include shrub characteristics (N-fixers vs. non-fixers) and positive effects of higher precipitation on this type of facilitation to characterize plant interactions along stress gradients.