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The XXII International Grassland Congress (Revitalising Grasslands to Sustain Our Communities) took place in Sydney, Australia from September 15 through September 19, 2013.

Proceedings Editors: David L. Michalk, Geoffrey D. Millar, Warwick B. Badgery, and Kim M.

Broadfoot

Publisher: New South Wales Department of Primary Industry, Kite St., Orange New South Wales, Australia

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Effects of nitrogen supply and nitrogen form on intrinsic water-use efficiency in temperate, semi-natural grasslands under rising atmospheric CO₂

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Keywords: C₃ grassland, ammonium, nitrate, long-term trends, Park Grass Experiment, carbon isotope discrimination.

Introduction

Carbon uptake and water loss of plants are controlled by the regulation of carbon assimilation rate (A) and stomatal conductance (g_s). Any changes in these parameters under rising atmospheric CO₂ concentration (c_a) influence plant water-use efficiency and can affect carbon and water relations in grassland ecosystems. Time-series analyses of intrinsic water-use efficiency (W_i) of C₃ grassland vegetation during the 20th century have shown that carbon uptake relative to water loss generally increased (Köhler *et al.* 2010, 2012; Barbosa *et al.* 2010). Short-term experiments suggest that nitrogen (N) supply (Stitt and Krapp 1999) and N form (Bloom *et al.* 2011) also play a role.

We hypothesize that any increase in W_i should be stronger in swards with high N availability and with ammonium (NH₄)-N instead of nitrate (NO₃)-N fertilization.

Methods

Stable carbon isotopes and intrinsic water-use efficiency

W_i ($=A/g_s$) is a physiological efficiency reflecting the leaf-level relationship between CO₂ uptake and transpiration at standard humidity. It can be derived from stable carbon isotopes by using the Farquhar model of carbon isotope discrimination ($^{13}\Delta$) during C₃ photosynthesis (Farquhar *et al.* 1989) and measurements of carbon isotope composition ($\delta^{13}C$) in plant material and atmospheric CO₂.

The Park Grass Experiment and analysed samples

The Park Grass Experiment at Rothamsted (Hertfordshire, England) is a long-term fertilization experiment on grassland and has been running since 1856. $\delta^{13}C$ was measured in samples of grassland vegetation (available from the Rothamsted Sample Archive) from 16 plots with different nutrient supply, soil pH and botanical composition. The sample period covered 95 years (1915-2009), during which c_a increased by 86 ppm. Nutrient supply on the plots differed in the form and amount of applied N [nil, 48, 96 (NO₃ and NH₄ plots) or 144 (NH₄ plots only) kg/ha/year], and the amount of P (nil or 35 kg/ha/year) and K (nil or 225 kg/ha/year). Soil pH varied between 3.6 and 5.9 on the un-

limed subplots and between 6.2 and 7.2 on the limed subplots (average values for 1995-2002).

Statistical analysis

The $^{13}\Delta$ data were analysed using a multiple linear regression model with c_a and plant available soil water as explanatory variables. W_i was derived from the modelled $^{13}\Delta$ values, and the change in W_i from 1915 to 2009 (ΔW_i) was studied (pooled and separately for limed and unlimed subplots) in relation to N supply.

Results

Changes in $^{13}\Delta$ per 100 ppm change in c_a varied between -1.0‰ and +0.9‰ on the 16 plots. Thus, the increase in W_i from 1915 to 2009 varied between 6.9 and 25.5 $\mu\text{mol/mol}$. When all 16 treatments were analysed together, no significant relationship was found between the change in W_i and the amount of applied N plus N from biological N-fixation (Fig. 1a, $P = 0.1$). A significant relationship was found for the limed NO₃-N plots ($P < 0.05$), but not for the unlimed ones ($P = 0.6$) (Fig. 1b). No significant relationship was found for the NH₄-N plots (limed: $P = 0.5$, unlimed: $P = 0.1$) (Fig. 1c).

A significant relationship between the increase in W_i and N supply was only found for the limed NO₃-N plots as reported in Köhler *et al.* (2012). The highest increases in W_i were observed on the unlimed NH₄-N plots, but no significant relationship with N supply could be found. In contrast to our hypothesis the increases in W_i on the limed NH₄-N plots were lower than on the limed NO₃-N plots. The difference between NO₃-N and NH₄-N plots and limed and unlimed subplots indicates that other factors may play a role. A recent study suggests that botanical composition may affect the response of W_i (Köhler *et al.* 2012). This may be due to the greater responsiveness of grasses and will be investigated in future work. The average percent-contribution of grasses to sward biomass varied between 49% and 99% and increased significantly ($P < 0.01$) with decreasing soil pH.

Conclusion

Besides N supply and N form, multiple factors may influence the response of W_i to rising c_a in terrestrial ecosystems

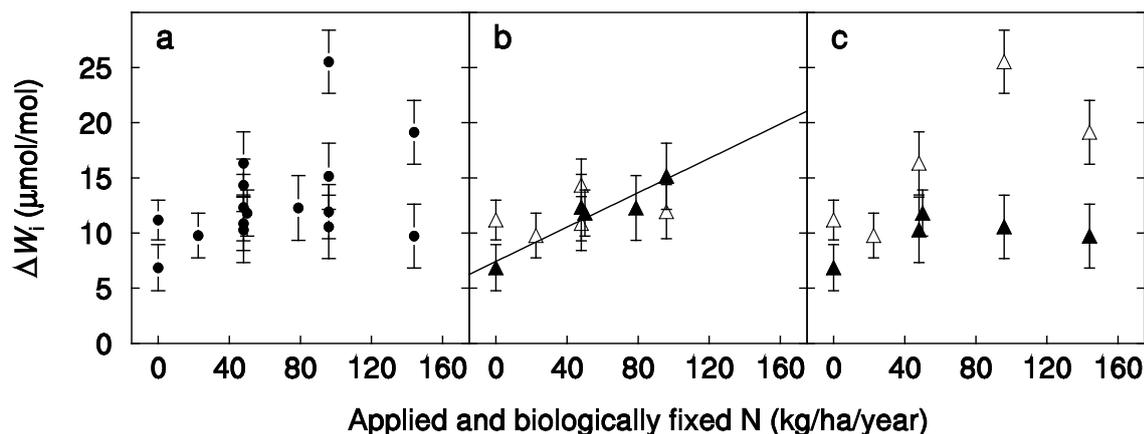


Figure 1. Relationship between the absolute change in W_i from 1915 to 2009 (ΔW_i , $\mu\text{mol/mol}$) and the amount of applied plus biologically fixed N (kg/ha/year), presented for (a) all plots, (b) $\text{NO}_3\text{-N}$ and (c) $\text{NH}_4\text{-N}$ plots and their limed (\blacktriangle) and unlimed (\triangle) subplots. The same data from the controls and the PK-only plots are used in all three graphs. The black line is the linear regression for the limed $\text{NO}_3\text{-N}$ plots ($y = 7.43 + 0.08x$, $P < 0.05$, $R^2 = 0.9$). Error bars represent the standard error.

directly or indirectly, *e.g.* through changes in botanical composition. Our understanding of these factors and their interactions needs to be improved to better predict future responses of grassland ecosystems to rising atmospheric CO_2 .

Acknowledgements

This study was supported by the Deutsche Forschungsgemeinschaft (DFG) (SCHN 557/5-1). We thank the Lawes Agricultural Trust for access to the archived samples and the BBSRC (UK) for support under the Institute National Capabilities programme grant.

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