Long-term effect of fertilisation on the composition of plants with different ecological strategies in Rengen Grassland Experiment

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Abstract

The dynamic of grassland vegetation is driven by varying responses of plants with different strategies to nutrient availability, particularly under different fertilisation regimes. To gain insights in these responses, the cover of individual plant species with different strategies was estimated over a 10-year study period (2005–2014) in the long-term Rengen Grassland Experiment, Germany (1941). The experiment is arranged in a randomised block design with five treatments and five replicates. The treatments include calcium (Ca); Ca and nitrogen (N); Ca, N and phosphorus (P); Ca, N, P, and potassium chloride (KCl); Ca, N, P and potassium sulphate (K_2SO_4); and one unfertilized control. All treatments are cut twice a year in late June/early July and mid-October. Fertilisation regimes influenced plant strategy composition over time. Plant species with S-strategy (stress-tolerant) and R-strategy (ruderal) dominated in phosphorus-deficient treatments, while their cover declined in treatments with combined P, N and K application. In contrast, plant species with C-strategy (competitive) responded positively to enhanced nutrient availability, particularly in nutrient-enriched plots with P application. The findings highlight the importance of optimising fertilisation levels to balance biomass production for agriculture with biodiversity conservation in grassland ecosystems.

Keywords: competition, nitrogen, phosphorus, potassium, treatments

Introduction

Grassland ecosystems consist of plant species exhibiting three primary ecological strategies as defined by Grime's C-S-R framework: S-strategy (stress-tolerant), R-strategy (ruderal), and C-strategy (competitive), which are strongly influenced by nutrient availability, particularly phosphorus (P), nitrogen (N), and potassium (K). High-input NPK fertilisation typically promotes C-strategy species, leading to shifts in species diversity and competitive interactions among plants, while reduced phosphorus application favours plants with S- and R-strategy (Maliniemi *et al.*, 2019; Dietrich *et al.*, 2024). However, the long-term development of plant ecological strategies under continuous fertilisation remains poorly understood. To address this knowledge gap, we analysed a decade-long dataset from the Rengen Grassland Experiment, one of Europe's longest-running fertilisation experiment, to assess how sustained nutrient enrichment influences development of plant strategies.

Materials and methods

The RGE was established in 1941 in extensively grazed heathland in the Eifel mountains (Germany, 50°13′N, 6°51′E; 475 m above sea level). The mean annual temperature is 6.9°C (Rengen meteorological station). The mean annual precipitation is 811 mm. The soil is classified as a Stagnic Camisole.

The experimental area was mown twice per year (in late June/early July and October) since 1962. The experiment is arranged into five randomised blocks with five fertilised treatments (applied nutrients in kg ha^{-1}) B: Ca (Ca = 715, magnesium (Mg) = 67); C: Ca/N (Ca = 752, N = 100, Mg = 67); D: Ca/N/P (Ca = 936, N = 100, P = 35, Mg = 75); E: Ca/N/P/KCl (Ca = 936, N = 100, P = 35, K = 133, Mg = 90); F: Ca/N/P/K_2SO_4 (Ca = 936, N = 100, P = 35, K = 133, Mg = 75) and one control (not fertilised) treatment (A). The percentage cover of all vascular plant species was estimated visually from the central area (1.8 × 3.2 m) of each plot. Nomenclature of vascular plant species follows the regional flora classification (Rothmahler *et al.*, 2000). C-S-R strategy values for each plot were calculated by weighing the mean C, S, and R values of each vascular plant species according to

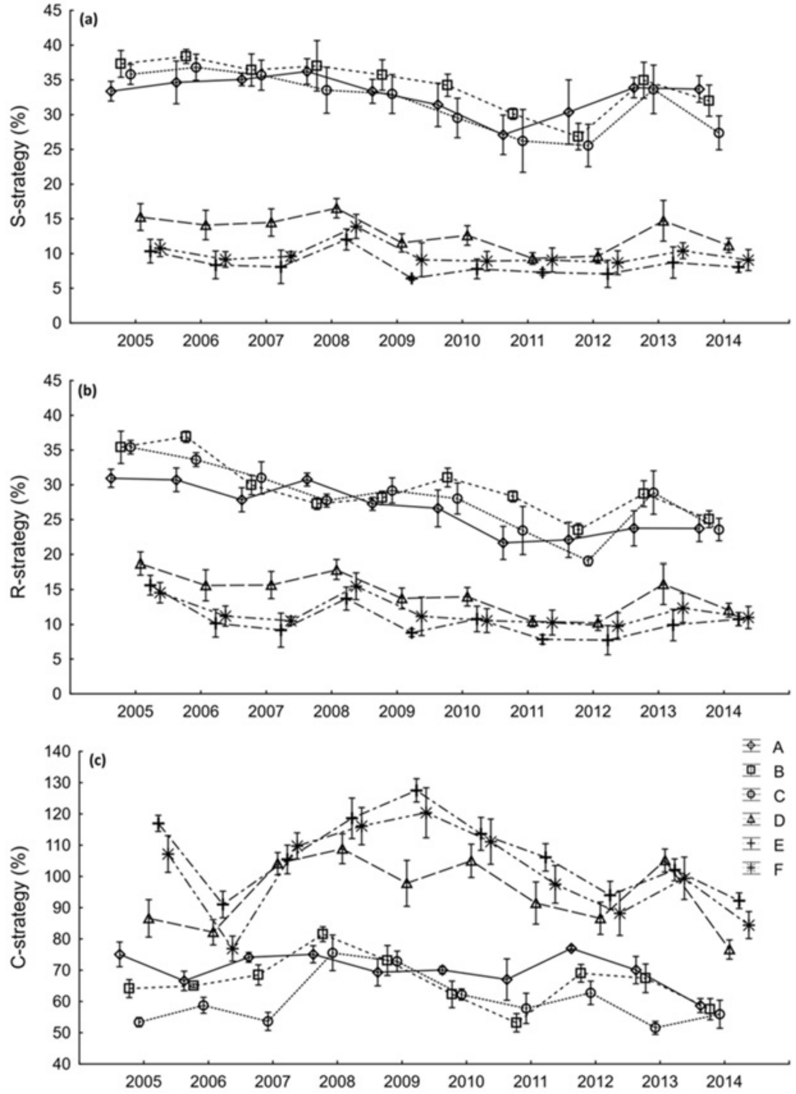

Figure 1. The mean cover (%) of plant species with (a) S-strategy; (b) R-strategy; (c) C-strategy in investigated treatments in the years 2005–2014. Treatment abbreviations are explained in the materials and methods section.

Table 1. Results of the general linear mixed-effects models (GLMM).

Tested variable	Metric	Treatment	Year	Treatment×Year
S-strategy (%)	*F*-ratio	501.9	10.8	0.7
	P-value	<0.001	<0.001	0.942
R-strategy (%)	*F*-ratio	174.8	11.5	1.4
	P-value	<0.001	<0.001	0.053
C-strategy (%)	*F*-ratio	75.91	7.34	2.63
	P-value	<0.001	<0.001	<0.001

F ratio, *F* statistic for the test of particular analysis; *P*-value, obtained probability value.

its cover, following Rothmahler *et al.* (2000). General linear models (GLMs) were used to test effect of treatments on plant strategies.

Results and discussion

The type of treatment and year significantly affected the cover (%) of plant species with S-strategy, R-strategy and C-strategy (Figure 1 and Table 1).

There was a significant treatment x year interaction on the cover of plant species with C-strategy, but not for the species with R and S-strategy (Table 1). The mean cover (%) of S-strategy and R-strategy species was higher in treatments without application of phosphorus (A–C) and lower in treatments with combined application of phosphorus, nitrogen and potassium (D–F) (Figure 1). In contrast, the mean cover (%) of plant species with C-strategy (%) was higher in treatments with combined application of phosphorus, nitrogen and potassium (D–F) and lower in phosphorus-deficient treatments (A–C) treatments. The dominance of C-strategy species under phosphorus fertilisation suggests enhanced competitiveness, likely driven by intensified light competition due to nutrient enrichment (Massey *et al.*, 2015). In contrast, the higher cover of S- and R-strategy species in phosphorus-deficient plots indicates their adaptation to low-nutrient conditions, where reduced competition allows their persistence (Maliniemi *et al.*, 2019; Dietrich *et al.*, 2024).

Conclusions

The decade-long dataset from the Rengen Grassland Experiment revealed that sustained nutrient enrichment (combined application of phosphorus, nitrogen and potassium) significantly alters plant species composition by promoting competitive species while suppressing stress-tolerant and ruderal species. These findings highlight the pivotal role of different fertilisation regimes in shaping plant functional dynamics and provide valuable insights for optimising grassland management to balance agricultural productivity with biodiversity conservation.

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References

Dietrich H., Pöschl U., Schmid M., and Koller R. (2024) Plant roots affect free-living diazotroph communities in temperate grassland soils despite decades of fertilization. *Nature Communications Biology* 7, 846.

Maliniemi T., Kalliola R., Rautio P., and Rikkinen J. (2019) Site fertility drives temporal turnover of vegetation at high latitudes. *Ecology and Evolution* 9, 10457–10467.