Productivity and sustainability influenced by biodiversity in grassland ecosystems

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The functioning and sustainability of ecosystems may depend on their biological diversity.\(^a\) Elton's\(^b\) hypothesis that more diverse ecosystems are more stable has received much attention,\(^1,2,4,7,10-14\) but Darwin's proposal\(^6\) that more diverse plant communities are more productive, and the related conjectures\(^4,5,6,17\) that they have lower nutrient losses and more sustainable soils, are less well studied.\(^4,5,17,18\) Here we use a well-replicated field experiment, in which species diversity was directly controlled, to show that ecosystem productivity in 147 grassland plots increased significantly with plant biodiversity. Moreover, the main limiting nutrient, soil mineral nitrogen, was utilized more completely when there was a greater diversity of species, leading to lower leaching loss of nitrogen from these ecosystems. Similarly, in nearby native grassland, plant productivity and soil nitrogen utilization increased with increasing plant species richness. This supports the diversity–productivity and diversity–sustainability hypotheses. Our results demonstrate that the loss of species threatens ecosystem functioning and sustainability.

The diversity–productivity hypothesis is based on the assumption that interspecific differences in the use of resources by plants allow more diverse plant communities to utilize more fully limiting resources and thus attain greater productivity.\(^6,8,17,18\) A related hypothesis is that nutrient leaching losses from ecosystems should be a decreasing function of plant diversity because of greater nutrient capture and/or immobilization in more diverse ecosystems.\(^4,5,7\) Taken together, these lead to the diversity–sustainability hypothesis; that the sustainability of soil nutrient cycles and thus of soil fertility depends on biodiversity. But the relationships between biodiversity and ecosystem functioning remain controversial.\(^3,15,13,18-23\) because existing field data are from studies that lacked direct experimental control of biodiversity or sufficient replication. Only direct control of diversity allows attribution of responses to diversity rather than to other correlated factors.\(^1,2,18-23\) Moreover, the species composition of plots must be randomly determined to avoid biases caused by the traits of particular species.\(^19,22\)

Here we report results of a field experiment in which the number of plant species was experimentally controlled (Fig. 1 legend). Our 147 plots, located on nitrogen-limited soil,\(^2\) were planted with either 1, 2, 4, 6, 8, 12, or 24 species. The species assigned to each plot were chosen by a separate random draw of the appropriate number of species from a pool of 24 North American prairie species. The impacts of diversity on plant productivity, nutrient capture and nutrient leaching were observed during the second year of growth. We also sampled a native grassland to determine the relationships between these variables in an undisturbed mature ecosystem.

Treatments created an experimental biodiversity gradient. Plant species richness, Shannon diversity (H'), and effective species richness (e,\(^e\) Fig. 1a) were all significantly correlated with the number of species seeded into the plots (Pearson's r = 0.81, r = 0.74, r = 0.75, respectively; n = 147, P < 0.001 for all). Two measures of peak standing crop (our estimate of plant productivity) were positively correlated with the species-richness treatment (total plant cover; r = 0.39, n = 147, P < 0.001, Fig. 1b; biomass estimated by light penetration; r = 0.27, n = 147, P < 0.001). Both estimates were similarly dependent on observed plot species richness (r = 0.55, r = 0.42, n = 147, P < 0.001 for both) and effective species richness (r = 0.29, r = 0.29, n = 147, P < 0.001 for both). Thus, greater plant diversity led to greater productivity during the second year of ecosystem establishment.

Rooting-zone extractable soil NO\(_3\) was a decreasing function of species richness (Fig. 1c). Extractable NH\(_4\) had a similar pattern (r = -0.18, n = 147, P = 0.03). This indicates that more species-rich plots more fully utilized soil mineral nitrogen, the main limiting resource.\(^2\) Below the rooting zone, soil NO\(_3\) concentrations

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<table>
<thead>
<tr>
<th>TABLE 1</th>
<th>Factors influencing plant total cover (productivity) in the biodiversity experiment</th>
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</thead>
<tbody>
<tr>
<td>Variable</td>
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<tr>
<td>Intercept</td>
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<tr>
<td>Species richness</td>
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<tr>
<td>Rooting zone NO(_3)</td>
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<td>Rooting zone NH(_4)</td>
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<td>Root mass</td>
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</table>

Multiple regression of total plant cover (dependent variable) on listed variables, each measured in all 147 plots. Overall F\(_{145} = 28.5, P < 0.0001, R^2 = 0.45\).

<table>
<thead>
<tr>
<th>TABLE 2</th>
<th>Factors influencing soil NO(_3) in the rooting zone in the biodiversity experiment</th>
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<td>Variable</td>
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<tr>
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<td>Plant total cover</td>
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<td>Root mass</td>
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</table>

Multiple regression of rooting zone soil NO\(_3\) on listed variables, each measured in all 147 plots. Overall F\(_{143} = 7.39, P < 0.0001, R^2 = 0.13\).
Fig. 1. a, Effective species richness is \( e^R \), where \( H' \) is the Shannon diversity index; \( e^R \) is the number of equally abundant species required to give the observed \( H' \). Curve is a simple second-order fit \( (R^2 = 0.60, n = 147, P < 0.001) \). b, Total plant cover is the sum of cover of all vascular species in a plot. Fitted curve is \( y = 27 + 3.64x/(5.48 + x) \), \( R^2 = 0.18, n = 147, P < 0.001 \). c, Soil nitrate (as mg of N per kg of dry soil) at 0–20 cm depth, where 79.8% of roots occur. Fitted curve is \( y = 0.17 + 0.02x \), \( R^2 = 0.22, n = 147, P < 0.001 \). d, Soil nitrate (as N) at 40–60 cm depth, where only 6.5% of roots occur. Fitted curve is \( y = 0.06 + 0.09/x + 0.02/x^2 \), \( R^2 = 0.14, n = 147, P < 0.001 \). All results plotted are means ± s.e.m.

METHODS. 147 plots, each 3 × 3 m, with 1-m walkways located at Cedar Creek in Minnesota, were randomly assigned to one of 7 species-richerich treatments: seeding plots in May 1994 to 1, 2, 4, 6 or 8 species (20 replicates each), 12 species (23 replicates), or 24 species (24 replicates). Species used were Achillea millefolium, Agropyron smithii, Andropogon gerardii, Aneronea cylindrica, Asclepias tuberosa, Aster azureus, Astragalus canadensis, Bouteloua gracilis, Buchloe dactyloides, Coreopsis palmata, Elymus canadenis, Euphorbia corollata, Eriophorum cristata, Lespedeza capitata, Liatris aspera, Panicum virgatum, Pentastemum purpureum, Poa pratensis, Rudbeckia hirta, Schizachyrium scoparium, Solidago nemoralis, Sorghastrum nutans, Sporobolus cryptandrus and Viola villosa. Species added to each plot were chosen by separate random draws from these 24 prairie perennials. Each plot received 10 g m\(^{-2} \) seed in total, with equal masses of each species. To prepare soils for planting, pre-existing vegetation was treated with herbicide and burned in August 1995. The upper 6 to 8 cm of soil was removed to reduce the seed bank, then plowed and repeatedly harrowed. Plots were watered twice a week and weeded from an elevated boardwalk. All responses to treatments were measured after two seasons of growth, in August 1995, time of peak standing crop, a measure of productivity in these grasslands. Standing crop was estimated using two ways. First, per cent cover of each species was determined in the same, predetermined 0.5 × 0.5-m plot in all plots for calculation of species richness, total plant cover, \( H' \) and \( e^R \). Second, light penetration through vegetation, measured 6 times per plot, was converted to biomass using a calibrated relationship. Soil nitrate and ammonium concentrations used 0.01 M KCl extractions, with two cores per plot. Root biomass data in regressions were from cores 5 cm diameter × 20 cm deep. Curves were chosen for simplicity and goodness of fit, and have much higher \( R^2 \) values than the corresponding Pearson (linear) correlations (see text).

were greater under low-diversity treatments (Fig. 1d), indicating greater leaching loss of soil nitrogen at lower plant diversity. Consistent with its low mobility in soil, NH\(_4\) showed no such dependence \( (r = 0.03, n = 147, P = 0.7) \).

In summary, this experiment shows that both plant productivity and resource utilization were significantly greater at higher plant diversity in these developing grassland ecosystems. The greater nutrient utilization at higher species diversity resulted in lower leaching loss of soil nitrogen, which should contribute to the sustainability of nutrient cycling and soil fertility in these ecosystems.

Native, undisturbed grassland showed similar relationships. Total plant cover increased significantly with plant species richness (Fig. 2a). The most species-rich plots had total cover of about 80%, compared with about 60% in our experiment, indicating that cover may continue to increase in our experiment. However, soil fertility (that is, the total soil nitrogen level, N) was higher in the native grassland than in the experiment (N: 686 mg kg\(^{-1}\) in the experiment; 345 mg kg\(^{-1}\) in the native grassland), which may explain this difference in plant cover. Rooting-zone extractable soil NO\(_3\) and NH\(_4\) were both negatively correlated with plant species richness in native grassland (NO\(_3\): \( r = -0.47, n = 120, P < 0.001 \), Fig. 2b; NH\(_4\): \( r = -0.28, n = 120, P < 0.001 \). As in the experiment (Fig. 1c), native vegetation showed higher variance in soil NO\(_3\) at lower species richness. Thus the relationships observed in our two-year field experiment also occurred in natural ecosystems, indicating that the effects of biodiversity observed during ecosystem establishment are maintained in mature ecosystems.

Compensatory competitive interactions\(^{2,14}\) might have played a role in causing these relationships in our experiment. Five species (Andropogon gerardii, Achillea millefolium, Bouteloua gracilis, Lespedeza capitata, and Rudbeckia hirta) had significantly \( (P < 0.01) \) greater abundance in higher-diversity plots than expected on the basis of their proportion in the seed mixture, indicating that, when present, they could compensate for poorly performing species. Multiple regression showed that total plant cover in the diversity experiment was negatively dependent on rooting-zone soil NO\(_3\) and positively dependent on root biomass (Table 1). But there remained a significant dependence of cover on species richness (Table 1), suggesting that additional factors related to species richness also were involved. Other multiple regressions showed that soil NO\(_3\) both in the rooting zone (Table 2) and below, was independent of plant cover and surface root biomass, but remained dependent on species richness. Further
work is needed to determine how interspecific morphological and physiological differences influence the dependence of ecosystem functioning on biodiversity in this and other ecosystems.

It is known that soil fertility and productivity influence diversity. Our results demonstrate that the converse is also true: in an experiment using initially homogeneous soils, plant diversity had a significant effect on productivity, nutrient use, and nutrient retention. The establishment and functioning of these grassland ecosystems depended on their species richness, with more diverse ecosystems being more productive and having lower nutrient losses than less diverse ecosystems. This extends earlier results to the field, providing direct evidence that the current rapid loss of species on Earth, and management practices that decrease local biodiversity, threaten ecosystem productivity and the sustainability of nutrient cycling. Observational, laboratory, and field experimental evidence supports the hypotheses that bio-

diversity influences ecosystem productivity, sustainability, and stability.