

with the observed range of  $V_P$  (7.2–7.5 km s<sup>-1</sup>). For instance,  $V_P$  calculated for a garnet granulite consisting of plagioclase (40 wt%), clinopyroxene (30%), orthopyroxene (10%) and garnet (20%) is 7.38 km s<sup>-1</sup>, and plagioclase (6.166 km s<sup>-1</sup>) and garnet (8.921 km s<sup>-1</sup>) have opposing effects on calculated  $V_P$  of rocks. Occurrences of mafic granulites as xenoliths are abundant in Kerguelen island. Indeed, in addition to the localities in the southeastern part of the islands, at least four localities were discovered and sampled in recent field seasons in the northeastern province, the Courbet peninsula. They indicate that a significant volume of granulite could exist beneath the islands and the northern Kerguelen plateau. The existence of a 'low-velocity mantle' zone beneath oceanic islands has been recognized beneath Marquesas<sup>37</sup>, and the progressive changes in seismic velocities have also been proposed for the Madagascar ridge<sup>38</sup> and the Crozet plateau<sup>39</sup>. Based on our finding, we speculate that mafic granulites can account for the observed seismic characteristics, and thus can be important constituents in those oceanic areas where large-scale magma production is predicted. If granulites represent underplated basaltic magmas and cumulates therefrom, which are otherwise not sampled by subaerial or submarine volcanics, their trace element and isotopic characteristics and geochronology are fundamentally important for understanding of the evolution of oceanic plateaus. □

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## Biodiversity and stability in grasslands

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ONE of the ecological tenets justifying conservation of biodiversity is that diversity begets stability. Impacts of biodiversity on population dynamics and ecosystem functioning have long been debated<sup>1–7</sup>, however, with many theoretical explorations<sup>5,6,8–11</sup> but few field studies<sup>12–15</sup>. Here we describe a long-term study of grasslands<sup>16,17</sup> which shows that primary productivity in more diverse plant communities is more resistant to, and recovers more fully from, a major drought. The curvilinear relationship we observe suggests that each additional species lost from our grasslands had a progressively greater impact on drought resistance. Our results support the diversity–stability hypothesis<sup>5,6,18,19</sup>, but not the alternative hypothesis that most species are functionally redundant<sup>19–21</sup>. This study implies that the preservation of biodiversity is essential for the maintenance of stable productivity in ecosystems.

The resistance of an ecosystem to perturbation and the speed of recovery, which is called resilience, are two important components of ecosystem stability<sup>6</sup>. Interest in the effects of biodiversity on stability has been heightened by the rapidly accelerating rate of species extinctions<sup>18,22,23</sup>. One view, the diversity–stability hypothesis, holds that species differ in their traits and that more

diverse ecosystems are more likely to contain some species that can thrive during a given environmental perturbation and thus compensate for competitors that are reduced by that disturbance<sup>5,6,7,12,18,19</sup>. This view thus predicts that biodiversity should promote resistance to disturbance. In contrast, the species-redundancy hypothesis asserts that many species are so similar that ecosystem functioning is independent of diversity if major functional groups are present<sup>19–21</sup>. An 11-year study of the factors controlling species composition, dynamics and diversity in successional and native grasslands in Minnesota<sup>16,17</sup> provides a test of the effects of biodiversity on ecosystem response to and recovery from a major perturbation. The study period included the most severe drought of the past 50 years<sup>24</sup> (1987–88), which led to a >45% reduction in above-ground living plant mass and a >35% loss of plant species richness in control plots<sup>24</sup>.

Nitrogen is the major nutrient limiting productivity in most terrestrial habitats<sup>25</sup>, including these Minnesota grasslands<sup>16</sup>. The species composition, diversity and functioning of these and many other ecosystems depend on the rate of nitrogen supply<sup>17,25,26</sup> and are thus being altered by increased atmospheric nitrogen deposition from agriculture and combustion of fossil fuels<sup>27–29</sup>. In 1982 we established, in four grassland fields, a total of 207 control and experimental plots in which plant species richness was altered through seven different rates of nitrogen addition<sup>16</sup>.

We measured resistance to drought by calculating, for each plot, the relative rate of plant community biomass change ( $\delta B/Bdt$ , yr<sup>-1</sup>; Fig. 1) from 1986, the year before the drought, to 1988, the peak of the drought. Values closer to zero imply greater drought resistance. For our 207 plots, drought resistance was a significantly ( $P < 0.0001$ ) increasing, but saturating, function of pre-drought plant species richness (Fig. 1). The greatest dependence of drought resistance on species richness occurred in plots

with nine or fewer species. The most species-rich plots produced about half of their pre-drought biomass during the drought, whereas the most species-poor plots produced only about one-eighth (Fig. 1).

Other characteristics of plots, such as the rate of nitrogen addition, total above-ground plant biomass, the proportion of total plant biomass from species with the C4 photosynthetic pathway, and differences in these variables among fields, were also correlated with species richness. Species composition and abundances also varied with species richness in these plots<sup>16,17</sup>. More than 90% of the plots that contained four or fewer plant species were dominated (>50% of plot biomass) by *Poa pratensis*, *Agropyron repens* or *Schizachyrium scoparium*. *Poa* and *Agropyron* are drought-sensitive C3 grasses, and *Schizachyrium* is a drought-resistant C4 grass. A partial correlation analysis that controlled for all of these potentially confounding variables (including the 1986 biomasses of these three species) showed a significant dependence of drought resistance on the natural logarithm of pre-drought species richness ( $r_{\text{partial}}=0.21$ ,  $n=207$ ,  $P<0.01$ ). Moreover, when all redundant, nonsignificant variables were removed using backwards elimination, species richness was retained, and its partial correlation with drought resistance was highly significant (Table 1).

The dynamics of individual species in our plots suggest that species richness led to greater drought resistance because species-

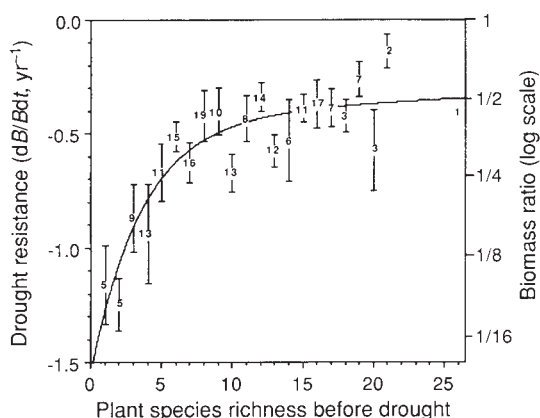


FIG. 1 Relationship between drought resistance of grassland plots and plant species richness ( $SR_{86}$ ) preceding a severe drought. Mean, standard error and number of plots with a given species richness are shown. Drought resistance was measured as  $dB/Bdt$  ( $yr^{-1}$ ), that is, as 0.5 ( $\ln$  [biomass<sub>1988</sub>/biomass<sub>1986</sub>]), where biomass<sub>1988</sub> is at the height of drought and biomass<sub>1986</sub> is for the year preceding drought. Biomass ratio (biomass<sub>1988</sub>/biomass<sub>1986</sub>; right-hand scale) shows the proportionate decrease in plant biomass associated with the  $dB/Bdt$  values. Because the correlation between species richness and drought resistance in our data was no longer significantly ( $P \leq 0.05$ ) positive when all plots with  $\leq 8$  or  $\leq 11$  species were ignored, we cannot reject the hypothesis that the relationship may reach a plateau. The solid curve ( $dB/Bdt = -1.13e^{-x/3.6} - 0.44e^{-x/11.0}$ , where  $x$  is  $SR_{86}$ ,  $r^2=0.22$ ,  $P<0.0001$ ), which was fitted to all 207 data points, is simply one of many that gave a significantly better fit than a straight line. A simpler equation ( $dB/Bdt = 0.304 \ln [SR_{86}] - 1.21$ ;  $r^2=0.21$ ,  $P<0.0001$ ) provided an equally good fit.

METHODS. These are described in detail in ref. 16. The 207 plots were located in existing vegetation in four grassland fields in Cedar Creek Natural History Area, Minnesota. Field A had been abandoned for 20 yr, field B for 31 yr and field C for 54 yr in 1988. Each contained 54 plots, each 4 × 4 m. Field D, a prairie opening in native savannah, contained 45 plots, each 2 × 4 m. Nine treatments: no nutrient addition, addition of macro- and micro-nutrients other than nitrogen, and seven treatments that received these nutrients but with seven different rates of nitrogen addition. Field D had five replicates per treatment, the others had six. Vegetation in each plot was sampled by clipping a different 0.3-m<sup>2</sup> subsection each year, sorting to species, drying and weighing. Species richness is the number of vascular species in a 0.3-m<sup>2</sup> sample. Biomass is total above-ground living plant mass ( $g\ m^{-2}$ ).

TABLE 1 Factors influencing drought resistance

Variable	Partial correlation coefficient	P
Field A intercept	-0.56	<0.0001
Biomass of <i>P. pratensis</i> (1986)	-0.39	<0.0001
Biomass <sub>1986</sub>	-0.36	<0.0001
$\ln (SR_{1986})$	0.29	<0.0001

Partial correlation of each listed variable with  $dB/Bdt$ , controlling for the other listed variables. Analyses used backwards elimination in multiple regression analyses to retain only variables that had significant ( $P<0.05$ ) partial correlations with  $dB/Bdt$ . The final multiple regression was highly significant ( $F=48.8$ ,  $n=207$ ,  $R^2=0.48$ ,  $P<0.0001$ ). Extensive residual analyses<sup>30</sup> were performed at each step. Candidate variables included  $\ln (SR_{1986})$ , logarithm of experimental plus atmospheric nitrogen addition, biomass<sub>1986</sub>, number of species of C3 and C4 plants in each plot, fraction of biomass comprised of C3 and C4 plants, dummy variables<sup>30</sup> for each field, and the biomass in 1986 of the three most common species in low species-richness (one to four species) plots (*A. repens*, *P. pratensis* and *S. scoparium*). The significant partial correlation for  $\ln (SR_{1986})$  means that the correlation of species richness with drought resistance does not arise through biomass, species composition or field effects<sup>31</sup>. Other multiple regressions examined change in species richness and biomass preceding drought, detrended annual variation in species richness and biomass preceding drought, and their interactions with  $SR_{1982}$  and biomass<sub>1982</sub>. No other multiple regression was significantly better than this one and all showed that partial correlations between species richness and drought resistance were statistically significant. Analyses using other measures of species diversity yielded similar results.

rich plots were more likely to contain some drought-resistant species. During this two-year drought, the increased growth of these drought-resistant species partially compensated for the decreased growth of other species.

A second component of stability is resilience, or the rate of return to pre-existing conditions after perturbation<sup>6</sup>. We calculated the deviation from pre-drought biomass as the natural logarithm of the ratio of plot biomass in 1989, 1990, 1991 and 1992 to average pre-drought biomass. For each of the four post-drought years, there were significantly negative intercepts and significantly positive slopes for regressions of these deviations on the

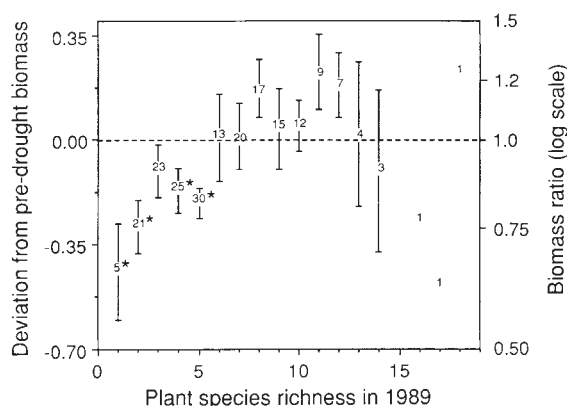


FIG. 2 Deviation of 1992 biomass from average (1982-1986) pre-drought biomass was measured as  $\ln$  [(biomass<sub>1992</sub>)/(average pre-drought biomass)]. Mean, standard error and number of plots are indicated for each level of species richness. Negative values mean that 1992 biomass was lower than pre-drought average. Biomass ratio is (biomass<sub>1992</sub>)/(average pre-drought biomass). Student's *t*-tests showed that plots containing 1, 2, 4 or 5 species differed significantly (\*  $P<0.05$ ) from their pre-drought average, but that plots with greater richness did not differ significantly from pre-drought averages.



TABLE 2 Factors influencing drought resistance

Variable	Partial correlation coefficient	P
Field A intercept	-0.39	<0.0001
Field B intercept	-0.30	<0.0001
Field C intercept	-0.20	0.003
ln (SR <sub>1989</sub> )	0.18	0.009
SR <sub>C3</sub>	-0.18	0.012
Biomass of <i>Schizachyrium</i> (1989)	-0.16	0.027
SR <sub>C4</sub>	-0.14	0.042

Partial correlations of each listed variable with deviation from pre-drought biomass, holding other listed variables constant. These seven variables were retained in multiple regression analysis of 1992 deviation from pre-drought biomass against the same candidate variables used in Table 1, but using 1989 values. Backwards elimination, with residual analysis, was used to retain only significant ( $P < 0.05$ ) variables. The overall regression had  $F = 14.0$ ,  $n = 206$ ,  $R^2 = 0.33$ ,  $P < 0.0001$ . SR<sub>C3</sub> is the number of C3 species and SR<sub>C4</sub> is the number of C4 species in plots in 1989. The significantly positive slope for ln (SR<sub>1989</sub>) and the significantly negative intercepts for fields A, B and C indicate that species-poor plots in these fields have not yet attained pre-drought biomass, whereas more species-rich plots have. Field D, a native grassland, recovered most rapidly, followed by field C, then B, then A, in order of successional age.

natural logarithm of 1989 species richness. These indicate that species-poor plots were still further from their pre-drought biomass than were species-rich plots in each of the four post-drought years.

By 1992, species-rich plots had returned to pre-drought biomass, but the most depauperate plots still had significantly less biomass than their pre-drought average (Fig. 2). When potentially confounding variables were controlled for, there was a significant partial correlation between drought recovery and the natural logarithm of 1989 species richness ( $r_{\text{partial}} = 0.184$ ,  $P < 0.01$ ,  $n = 207$ ). Moreover, when all redundant, nonsignificant variables were removed, species richness was retained, and its partial correlation was highly significant (Table 2). Thus, species-poor plots were both more greatly harmed by drought (Fig. 1 and Table 1) and took longer to return to pre-drought conditions (Fig. 2 and Table 2). The stand of native prairie was significantly more resilient than the three successional grasslands (Table 2).

Our results and earlier studies<sup>5,12,14,15</sup> support the diversity-stability hypothesis<sup>5</sup>, and show that ecosystem functioning is sensitive to biodiversity. Our results do not support the species-redundancy hypothesis because we always found a significant effect of biodiversity on drought resistance and recovery even when we controlled statistically for the abundances of C3 (often drought sensitive) and C4 (often drought resistant) plant functional groups (Table 1).

Our results show that ecosystem resistance to drought is an increasing but nonlinear function of species richness. This is expected from the mechanism underlying the diversity-stability hypothesis. Functional diversity should be a saturating function of species richness because, in species-rich ecosystems, additional species are more likely to be similar to existing species<sup>21</sup>. Thus, the progressive loss of species should have progressively greater impacts on ecosystem stability.

In addition to drought, grassland ecosystems experience periodic invasions of insect or mammalian herbivores, unusually late or early frosts, unusually wet or cool years, hail, fire, and other perturbations. Because different species are likely to perform best for particular combinations of these disturbances, the long-term stability of primary production in these and other<sup>12</sup> grasslands should depend on their biodiversity. Although we do not know how the stability of other ecosystems depends on

biodiversity, these results lend further urgency to pleas for the conservation of biodiversity. □

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## The role of partial occlusion in stereopsis

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MODELS of stereopsis typically assume that all the information about stereoscopic depth is contained in the disparity field, that is, the positional differences of image features that arise from surfaces visible to both eyes. But such models have difficulty in resolving image regions containing occlusions, because a portion of the occluded surface is visible to only one of the two eyes ('half-occlusions')<sup>1</sup>. Here I present displays revealing an unexpected relationship between interocular differences in image position and occluding contours. The partial occlusion of contours can give rise to both horizontal and vertical image differences that are not disparities. The results show that the visual system interprets these image differences as signalling the presence of occluding contours. Even when a single line segment serves as a binocular target, subjective contours form that can appear both oriented and in depth. These local subjective contours have a strong tendency to interact cooperatively and form global contours not present in the monocular images. These and other findings<sup>2–4</sup> show that stereoscopic processing actively decomposes vertical and horizontal image differences into disparities and half-occlusions. The two sources of information are complementary: while disparity provides relative depth information about surface features visible to both eyes, half-occlusions provide information to segment the visual world into coherent objects at object boundaries.