BIODIVERSITY: POPULATION VERSUS ECOSYSTEM STABILITY[1]

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Abstract. The relationships between biodiversity and stability were determined for both population and ecosystem traits in a long-term study of 207 grassland plots. Results demonstrate that biodiversity stabilizes community and ecosystem processes, but not population processes. Specifically, year-to-year variability in total aboveground plant community biomass was significantly lower in plots with greater plant species richness both for the entire 11-yr period and for the nine non-drought years. The change in total plant community biomass from before the drought to the peak of the drought was also highly dependent on species richness. For all three measures of total community biomass stability, multiple regressions that controlled for covariates showed similar significant relationships between plant diversity and stability.

In contrast, year-to-year variability in species abundances was not stabilized by plant species richness for either all years or non-drought years. This difference between species vs. community biomass likely results from interspecific competition. When climatic variations harm some species, unharmed competitors increase. Such compensatory increases stabilize total community biomass, but cause species abundances to be more variable. These results support both the predictions of Robert May concerning the effects of diversity on population stability and the diversity–stability hypothesis as applied to community and ecosystem processes, thus helping to reconcile a long-standing dispute.

Key words: biodiversity; climatic variability; compensation; competition; diversity–stability hypothesis; drought; grasslands; prairie; primary productivity; savanna; stability.

INTRODUCTION

Fragmentation, grazing, forestry, and nutrient deposition are decreasing the biological diversity of many of the earth's remaining semi-natural ecosystems (e.g., Ehrlich and Ehrlich 1981, Aerts and Berendse 1988, Wilson 1988, 1992, Ehrlich and Daily 1993). Elton (1958:145–153) suggested that decreased diversity would lead to decreased ecological stability and functioning, and presented several arguments in support of this. However, there has been continuing debate about the diversity–stability hypothesis (e.g., Gardner and Ashby 1970, May 1973, 1974, McNaughton 1977, 1985, Pimm 1979, 1984, Lawton and Brown 1993, Schultze and Mooney 1993, Vitousek and Hooper 1993, Givnish 1994, Tilman and Downing 1994). For instance, in a simple model of multispecies competition, May (1973) showed that population dynamics were progressively less stable as the number of competing species increased, and concluded that there need not be any relationship between diversity and stability. Gardner and Ashby (1970), DeAngelis (1975), Gilpin (1975), and Pimm (1979) reached similar conclusions using different models. In contrast, McNaughton (1977) presented data on plant productivity in the Serengeti that supported Elton. King and Pimm (1983)

modeled systems like McNaughton's and found that higher plant diversity generally led to greater biomass stability in response to changes in herbivory, just as McNaughton had observed. Similarly, Vitousek and Hooper (1993) suggested that the rates of many ecosystem processes could be increasing but saturating functions of species diversity.

Despite this controversy, there have been surprisingly few studies of the relationships between diversity and stability (Mellinger and McNaughton 1975, McNaughton 1977, 1985, Lepš et al. 1982, Ewel 1986, Berish and Ewel 1988, Ewel et al. 1991, Frank and McNaughton 1991, Tilman and Downing 1994). In this paper I report on a 13-yr study of plant species abundances, diversity, and production in 207 permanent Minnesota grassland plots that experienced great climatic variability, including a major drought in 1987 and 1988. I analyze the relationships between plant species richness and year-to-year variability in the abundances of both individual species and total plant community biomass. These analyses help reconcile the seemingly divergent predicted effects of biodiversity on population vs. ecosystem stability (Elton 1958, May 1973, McNaughton 1977). I also further analyze the relationships between plant species richness and drought resistance and resilience presented in Tilman and Downing (1994). The resilience analyses are expanded to control for the confounding effects of the size of the perturbation on recovery (Pimm 1984).

Because plant species richness was not directly controlled in this experiment, but rather differed among plots and fields and in response to nitrogen addition (Tilman 1993), detailed information on other factors that covaried with plant species richness is presented. This is important because correlations among variables in a multi-causal system, such as an ecosystem, are open to alternative interpretations. Such problems are minimized, but not eliminated, by multiple regressions that statistically control for variables that covary with species richness.

METHODS

In 1982, four fields at Cedar Creek Natural History Area were chosen for an experimental study of the effects of nitrogen on grassland productivity, species dynamics, and biodiversity. Methods are in Tilman (1987, 1993) and are only summarized here. Fields A, B, and C were unburned successional fields that had been abandoned from row crop farming for 14, 25, and 48 yr, respectively, in 1982. Field D was a prairie opening in native, never-farmed savanna and has been burned in the spring for 2 of every 3 yr starting in 1966 (Tester 1989, Faber-Langendoen and Tester 1993). In each field, an area fenced to reduce densities of mammalian herbivores (which otherwise increase after nutrient addition; Tilman 1983) was divided into plots, and plots randomly assigned to one of nine treatments. Fields A, B, and C each had 54 plots, each 4 × 4 m, with six replicates per treatment. Field D had 45 plots, each 2 × 4 m, with five replicates per treatment. Plots were separated by 1-m walkways. Experimental treatments (Tilman 1987) were (1) no nutrient addition (controls), (2) addition of all nutrients but N (i.e., of P, K, Ca, Mg, S, Na, and trace metals), and (3–9) addition of all nutrients but N in conjunction with one of seven different experimental rates of N addition (1, 2, 3.4, 5.4, 9.5, 17, or 27.2 $g \cdot m^{-2} \cdot yr^{-1}$ of N as NH_4NO_3). Nutrients were added annually in equal amounts in early spring (1–7 May) and early summer (23–30 June). In addition, all plots received ≈ 1 $g \cdot m^{-2} \cdot yr^{-1}$ of N via atmospheric deposition. The rates of N addition used in the remainder of this paper are the sum of experimental and atmospheric N addition. Fine-ground agricultural lime was added, as needed, to prevent changes in soil pH associated with NH_4NO_3 addition.

Aboveground vegetation in each plot was sampled by clipping a 10 × 300 cm strip at the soil surface. A different portion of each plot was sampled each year. All living vascular vegetation was sorted to species, dried, and weighed. Litter, including standing dead, was also dried and weighed. Sampling occurred during $\approx$5–14 July for Field A, 1–10 August for Field B, 10–26 August for Field C, and 26 August–4 September for Field D. This corresponds with the approximate time of peak aboveground standing crop in each field. The summed dry mass of all aboveground living vascular plant species from a harvest will be called "community

biomass," and should be approximately proportional to aboveground primary productivity. Relative abundance refers to the proportion that a species or functional group comprises of the aboveground community biomass of a plot. Species richness is the total number of vascular plant species per clip strip (of area 0.3 m²). Analyses that used diversity indices other than species richness (e.g., H' and $e^{H'}$) gave similar results, and are not presented here for brevity.

To determine root biomass, three 6.4 cm diameter × 20 cm deep soil cores were collected at 1-m intervals along the 3 m long clip strip in each plot immediately after clipping in 1987. Those from each plot were combined, gently washed in a sieve to remove soil, and roots were separated from other material. Each sample was dried and weighed to give an estimate of root biomass, expressed as grams per square metre.

Analyses were performed using SAS Version 6.09 (SAS Institute Incorporated 1989). All curves were fitted using least squares regression. Because apparent relationships between various measures of stability and species richness might be caused by factors that covaried with species richness, multiple regressions were used to control for such variables. The variables included in the multiple regressions were ones that covary with species richness and might be potential causes of differences in stability (e.g., community biomass, biomass of dominant species, biomass of the plant functional groups, root biomass, and root : shoot ratio). Climatic variables were not used because all plots experienced the same climate. As a further check on the possible role of species richness, backwards elimination was used to determine if species richness was retained in the subset of variables that all contributed significantly ($P \leq 0.05$) to the regression. In backwards elimination, the least significant variable is eliminated from a multiple regression, and a new multiple regression is performed, until all remaining variables are significant. Analyses of variance and multiple regressions used the General Linear Models routines. Multiple regressions included categorical variables to test for differences in intercepts among fields or other categorical variables.

Cumulative growing season precipitation was calculated as the total precipitation from 1 January to 1 August of each year. Potential evapotranspiration was calculated using the formulas of Thornthwaite and Mather (1955) for this same period. Growing degree days were estimated by subtracting 15°C from the daily average temperature and summing all positive differences over the growing season.

Of the 207 plots in this experiment, two are excluded as extreme outliers from analyses that used 1989–1993 data. This was caused by the presence in the 1992 and 1993 clipped strip of one plot of an extremely large individual of *Helianthus gigantea* and by the presence in the 1989 clipped strip of the other plot of a clone of the shrub *Corylus americanus*. These caused these

plots to have extreme year-to-year variability in biomass (cv), even though all the other years had variability similar to that of other plots.

Year-to-year variability in community biomass was measured three ways. The rate of change in community biomass in response to the 1987–1988 drought was calculated using the $\log_e$ of the ratio of community biomass in each plot at the peak of the drought in 1988 to that in 1986, just before drought (i.e., $\log_e$ [biomass$_{1988}$/biomass$_{1986}$]/2). This specific rate of change in community biomass from 1986 to 1988 (units of year^{-1}), called RGR$_{86-88}$, is a measure of drought resistance (Tilman and Downing 1994). The second measure was the coefficient of variation for community biomass (cv = 100·1 SD/mean) for each plot across all years. Because cv standardizes for the mean, it is less dependent on the mean than the standard deviation, and provides an index of year-to-year variation in community biomass relative to the mean. These cvs were calculated, on a plot-by-plot basis, using data on community biomass in each plot for all years from 1984 through 1994 and are called cv$_{84-94}$. cvs also were calculated using community biomass in a plot for all of the 1984 through 1994 period except the drought years of 1987 and 1988. These are called cv$_{ND}$ (for nondrought). Data for 1982 and 1983 were not used to reduce the possibility that results depended on initial dynamic responses to N addition.

cvs were also determined on a species-by-species basis for each plot, using the biomass of a species in a plot both over the period from 1984 through 1994 and for non-drought years. These are called cv$_{species-ALL}$ and cv$_{species-ND}$. Only common species, defined as those present in a plot for at least 9 out of the 11 yr, or 8 of 9 yr, respectively, were considered. Rarer species have higher estimated cvs because of the unavoidable sampling noise associated with their presence or absence in a given sample. Because of this, the cv of rarer species is dependent on the thoroughness of sampling and provides little information on population stability.

Resilience measures the rate of return toward equilibrium after a perturbation away from equilibrium. Drought resilience was quantified much as suggested by Pimm (1984), by calculating the difference between the community biomass of a plot in a given post-drought year and its pre-drought (1982–1986) average. This was divided by the difference between 1988 (the peak of the drought) and the pre-drought average to calculate "relative biomass deviation" for that year. This measures the proportion of the drought deviation that had not yet been recovered in a given post-drought year. A positive value indicates that a plot has not yet re-attained its pre-drought biomass, whereas a value of 0 indicates that a plot has re-attained its pre-drought mean. The $\log_e$ of this ratio was not used because many plots exceeded their pre-drought average community biomass during some post-drought years, and thus had negative values, for which $\log_e$ would be undefined.

Pearson correlation was used to determine if relative biomass deviation correlated with post-drought (1989) species richness.

RESULTS

Climate and plant community biomass

Because the third worst drought of the past 150 yr occurred during 1987–1988 (Tilman and El Haddi 1992), climatic variation was a major factor during this study (Fig. 1). There was a marked deficit in soil moisture during the drought (Fig. 1A) and 1988 was the hottest growing season of the study period (Fig. 1B). The 1992 and 1993 growing seasons were unusually cool (post-Pinatubo eruption) and included several late frosts (mid-June vs. the usual mid-to-late May), but differed in that 1992 was drier and 1993 was wetter. The 1990 growing season was unusually wet but with normal temperatures. This variation in climate was associated with variation in community biomass, shown for all plots receiving no added N in the three successional fields (Fig. 1C) and savanna (Fig. 1D). The greatest decrease in community biomass was associated with the 1987–1988 drought, and the greatest increases with the end of the drought in 1989 and with the unusually cool and wet growing season of 1993 (Fig. 1C, D). The first five growing seasons, 1982–1986, had near-normal precipitation and temperatures, and similar plant community biomass in the three successional fields. The gradual increase in community biomass in Field D may result from N fixation by legumes freed from deer browsing (Ritchie and Tilman 1995). The next seven growing seasons had major deviations of precipitation and/or temperature from long-term means, and major changes in community biomass.

Effects of nitrogen addition

Nitrogen addition established an experimental gradient along which community biomass increased highly significantly (Pearson correlation positive with $P <$ 0.01, $N = 205$) for all years of the study except during the 1988 drought (Fig. 2A), which was the only year in which treatments did not differ in community biomass (1988 ANOVA: $F = 0.57$, df = 7, 199, $P = 0.78$). On average across all treatments, the most abundant species were *Agropyron repens, Poa pratensis, Schizachyrium scoparium,* and *Andropogon gerardi.* Their relative abundances (Tilman 1987) and abundances of major plant functional groups (Fig. 2B) also changed along the N gradient. On average across all plots, C_3 grasses and woody species (mainly vines and shrubs) had increasingly greater relative abundance at higher rates of N addition, whereas the relative abundances of legumes and C_4 grasses decreased along the gradient. Plant species richness declined along the N gradient for each year except the first (Fig. 2C shows 4 yr). The four fields also differed in average species richness, with plots receiving no experimental N addition in
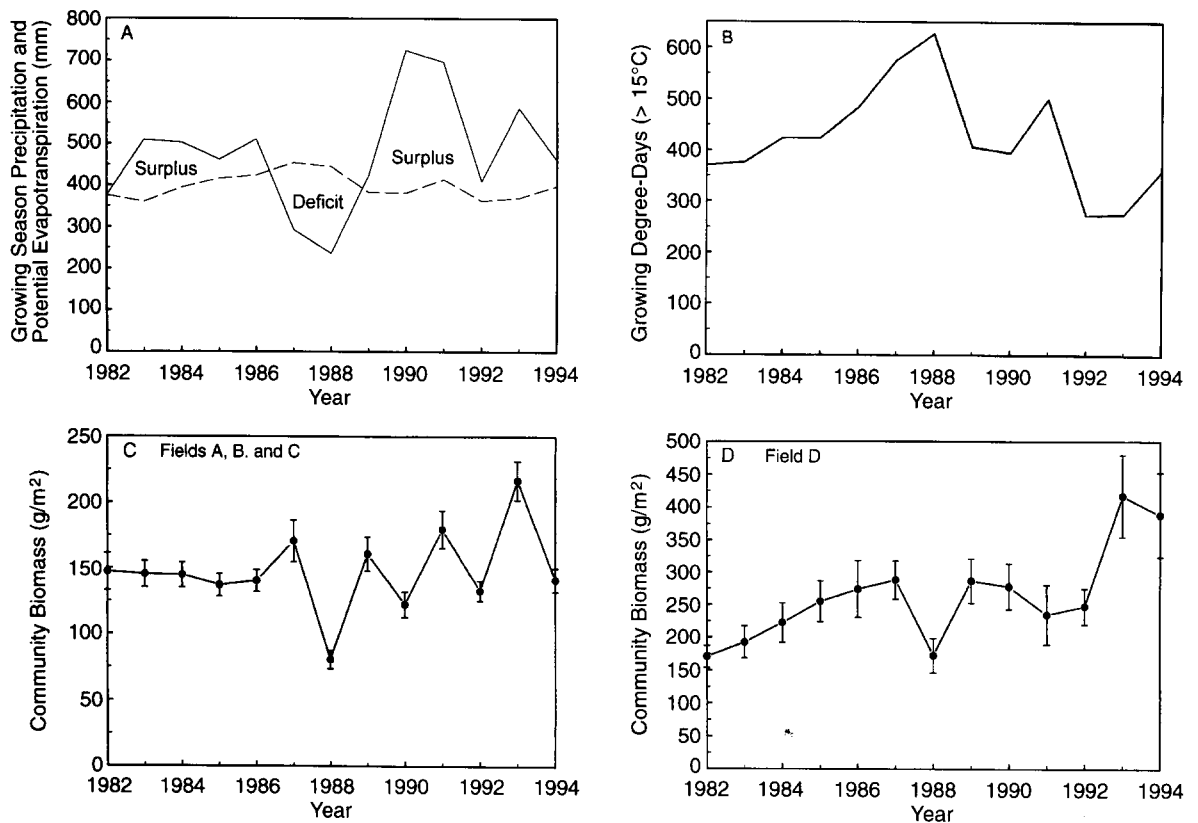
FIG. 1. (A) Growing season precipitation (solid line) and potential evapotranspiration (dashed line) shows periods of deficit or surplus in soil moisture; (B) growing degree-days for each growing season calculated as summed degrees >15°C for each day that this occurred; (C) average total aboveground living vascular plant biomass (community biomass) each year (± 1 SE) for the 42 plots not receiving N fertilizer in the three successional grassland fields; (D) as in (C), but for the field of native savanna.

Field A averaging 9.5, Field B averaging 8.6, Field C averaging 12.6, and Field D averaging 14.9 species/0.3 m² for 1982 through 1994.

Year-to-year changes

On average across all 46 plots to which no N was added experimentally, the relative abundance of C_4 grasses was fairly constant until the drought, increased through 1990, and declined toward pre-drought levels by 1994 (Fig. 3A). C_3 grasses increased from 1982 through 1986, decreased somewhat during the drought, and then re-attained their pre-drought maximum by 1994. Forb relative abundance declined sharply from 1982 through 1985 and remained relatively constant afterwards. Legumes were initially rare, increased from 1982 through 1986, declined somewhat during the drought, and increased again after the drought. Woody plants were always rare and showed no clear pattern of change.

For plots receiving a moderate rate of N addition (4.4 g·m⁻²·yr⁻¹; Fig. 3B), C_3 grasses initially increased in relative abundance, declined somewhat during the drought, and then increased. C_4 grasses initially declined, increased during the drought and through 1990,

and then declined. Forbs had a somewhat similar pattern, but increased during 1993 and 1994 (Fig. 3B). For plots receiving a high rate of N addition, C_3 grasses increased throughout the 12 yr, except during the drought (Fig. 3C). C_4 grasses and forbs showed the opposite pattern. Species richness was relatively constant in plots receiving no added N until 1986, fell 37% during the drought, and did not re-attain its pre-drought average until 1993 (Fig. 3D). Species richness in plots receiving moderate and high N addition declined until and through the drought, and then increased.

Species richness and plant community biomass dynamics

A. Responses to drought.—Species richness in 1986, the year before the drought, was used to group plots as containing one to four, five or six, seven or eight, nine or ten, eleven or twelve species, etc., with the last group being all plots containing 17–26 species. The first and last groups were broader to allow them to include about as many plots as the other groups. Mean and standard error of community biomass for each group may be compared with the pre-drought (1982–1986) mean biomass (dashed line) to visualize how the
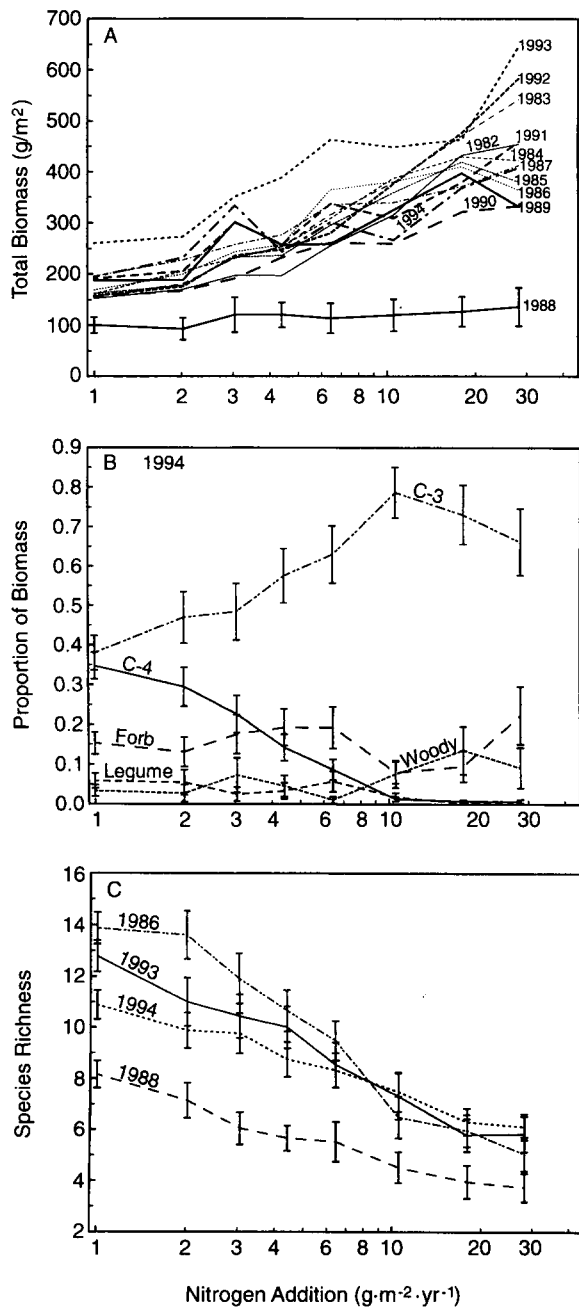
FIG. 2. (A) Average total aboveground living vascular plant biomass (community biomass) for each year is graphed against the (logscale) annual rate of nitrogen addition (which includes fertilizer N and atmospheric addition); (B) proportion of community biomass that is in (_ . .) C_3 grasses, (———) C_4 grasses, (– – –) legumes, (——) other forb species, (········) or woody species, graphed against N addition rate. (C) Average species richness/0.3-m² clip strip ($\pm$ 1 SE) graphed against N addition rate, for four years of the study.

biomass decline during drought, and its recovery, depended on species richness (Fig. 4).

The ratio of community biomass in each plot in 1988 to that in 1986 (biomass$_{1988}$/biomass$_{1986}$) was used to

quantify the biomass decline during the drought. Mean and standard error of this ratio were calculated for each level of 1986 species richness (SR_{86}), and graphed on a log scale. This shows that species-rich plots suffered lower proportional declines in community biomass during the drought than did species-poor plots (Fig. 5; Tilman and Downing 1994). RGR_{86-88}, an index of drought resistance, is shown on the other axis. The fitted curve ($RGR_{86-88} = -1.13e^{-SR/36} - 0.44e^{-SR/110}$), where SR is 1986 species richness ($r^2 = 0.22$, $N = 207$, $P < 0.001$) is one of many providing statistically indistinguishable fits (Tilman and Downing 1994).

Because many factors other than SR_{86} also varied among plots, multiple regressions were used to control for additional variables to determine if a significant dependence of RGR_{86-88} on species richness remained (Table 1; see also Tilman and Downing 1994). The variables used were $\log_e(SR_{86})$, community biomass$_{1986}$, $\log_e$(community biomass$_{1986}$), C_3 species richness in 1986, C_4 species richness in 1986, $\log_e$(nitrogen addition rate), biomass$_{1986}$ of Agropyron repens, biomass$_{1986}$ of Andropogon gerardi, biomass$_{1986}$ of Poa pratensis, biomass$_{1986}$ of Schizachyrium scoparium, biomass$_{1986}$ of C_3 grasses, biomass$_{1986}$ of C_4 grasses, biomass$_{1986}$ of legumes, biomass$_{1986}$ of other forbs, biomass$_{1986}$ of woody plants, biomass$_{1987}$ of roots, root: shoot ratio$_{1987}$, and categorical variables for Fields A, B, C, and D. RGR_{86-88} was significantly positively dependent on $\log_e(SR_{86})$ in the full multiple regression ($P = 0.012$). Species richness was retained as a significant variable in the simplified multiple regression obtained by backwards elimination (Table 1).

The relative biomass deviation (deviation, for a given year, of plot biomass from its pre-drought average divided by its deviation during the drought) was weakly negatively correlated with post-drought species richness (SR_{89}) in 1989 ($r = -0.13$, $N = 203$, $P = 0.07$) and significantly so in 1990 ($r = -0.18$, $N = 200$, $P = 0.01$), but not in 1991 ($r = -0.10$, $N = 204$, $P = 0.15$) or 1992 ($r = 0.01$, $N = 204$, $P = 0.86$). The significantly positive intercept and significantly negative slope of 1990 indicate that the rate of community biomass recovery following drought (i.e., resilience) was dependent on species richness that year. However, when additional variables, similar to those described in the preceding paragraph, were included in multiple regressions, there were no significant effects of 1989 species richness on resilience for either 1989 ($P = 0.62$) or 1990 ($P = 0.37$). Species richness was not retained as significant (with $P < 0.05$) in backwards eliminations for either year.

B. Year-to-year biomass variability and species richness.—The coefficient of variation in community biomass for 1984 through 1994 (CV_{84-94}) was significantly negatively correlated with plot average species richness (SR_{84-94}) for this same period ($P < 0.001$, $N = 205$) and significantly dependent on field ($P < 0.01$), but there was no field by SR_{84-94} interaction ($P = 0.12$). On
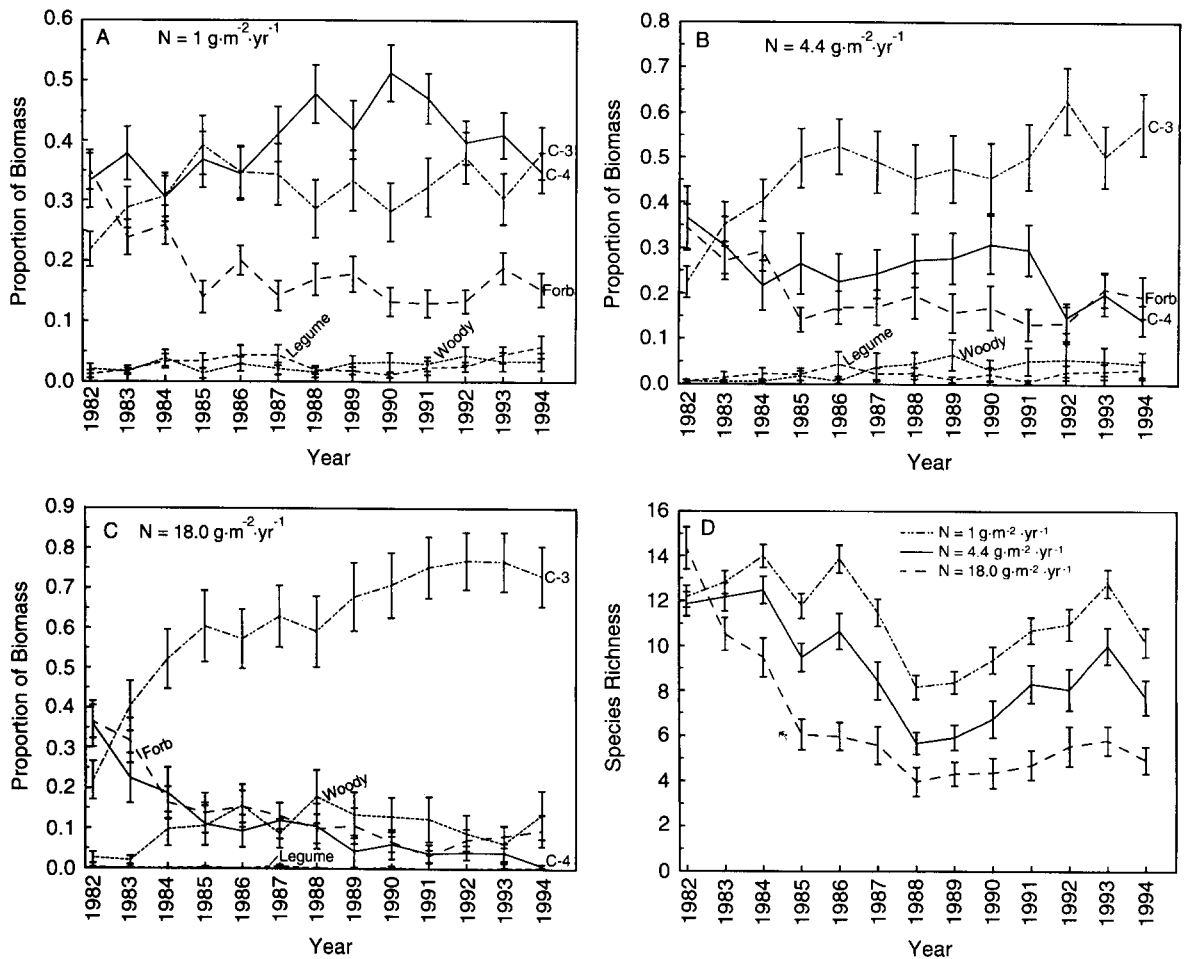
FIG. 3. (A–C) Year-to-year changes in across-field average (±1 SE) relative abundance of (‒ . .) C_3 grasses, (———) C_4 grasses, (- - -) legumes, (——) other forbs, and (········) woody plants, in plots receiving three different rates of N addition (N); (D) Average (±1 SE) species richness dynamics for these three rates of N addition.

a field-by-field basis, CV_{84-94} was significantly negatively correlated with SR_{84-94} in three of the four fields (Fig. 6). Multiple regression tested for the dependence of CV_{84-94} on SR_{84-94} when simultaneously controlling for the 1984 through 1994 averages, for each plot, of community biomass, biomass of *Agropyron repens,* of *Andropogon gerardi,* of *Schizachyrium scoparium,* of *Poa pratensis,* of C_3 grasses, of C_4 grasses, of legumes, of other forbs, and of woody species. In addition, regressions included log_e(rate nitrogen addition), log_e(community biomass$_{84-94}$), categorical variables for the four fields, root biomass in 1987, and root:shoot ratio in 1987. In the full multiple regression, CV_{84-94} was significantly negatively correlated with SR_{84-94} ($F_{1,204} = 7.51$, $P = 0.007$), indicating that there was less year-to-year community biomass variability in more species-rich plots. SR_{84-94} was retained as a highly significant variable in the model derived via backwards elimination (Table 2). Similar statistically significant results were obtained when data for 1982 through 1994 were used.

C. Variability in non-drought years.—The coefficient of variation in community biomass for non-drought years, CV_{ND}, was significantly negatively correlated with SR_{ND}, the average species richness for this same period ($P < 0.001$, $N = 207$), and depended on field ($P = 0.02$), but there was no $SR_{ND} \times$ field interaction ($P = 0.42$). On a field-by-field basis, CV_{ND} was significantly negatively correlated with species richness in Fields A and D but not in Fields B and C (Fig. 7). For all fields combined, a multiple regression that used variables analogous to the 19 that led to Table 2, but with data for non-drought years, revealed a highly significant negative dependence of CV_{ND} on species richness ($F_{1,204} = 14.92$, $P < 0.001$). CV_{ND} remained highly significant in the model derived via backwards elimination (Table 3).

Effects of other variables on stability

Most variables used in the multiple regressions did not significantly contribute to them (Tables 1–3). This was surprising for the rate of nitrogen addition because
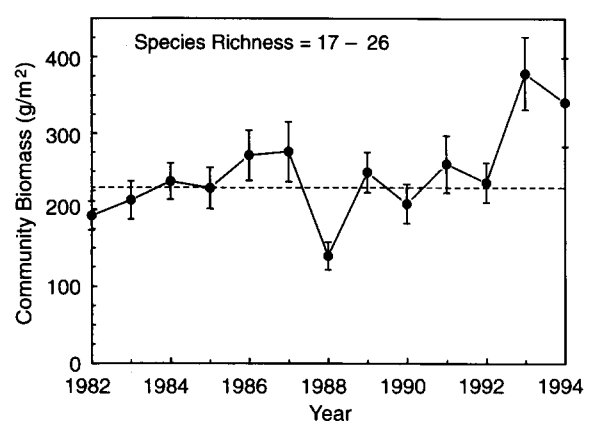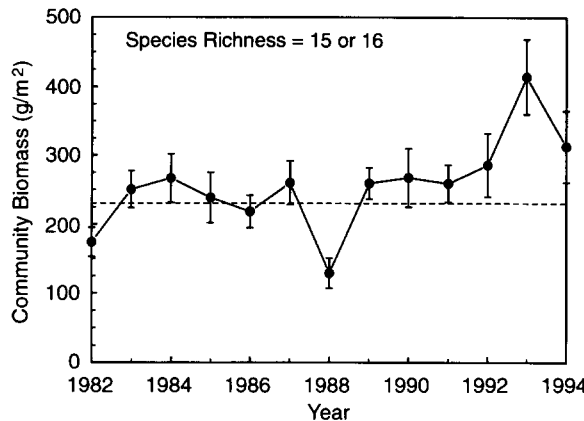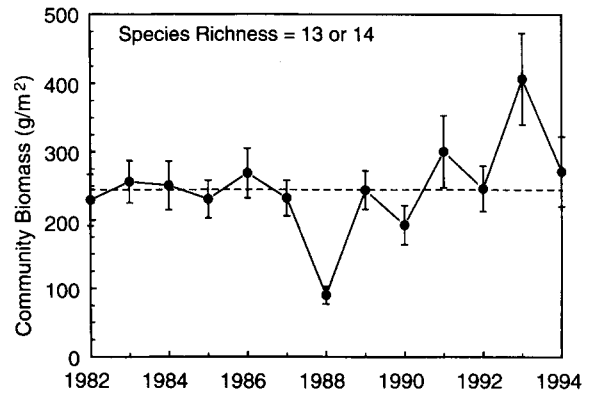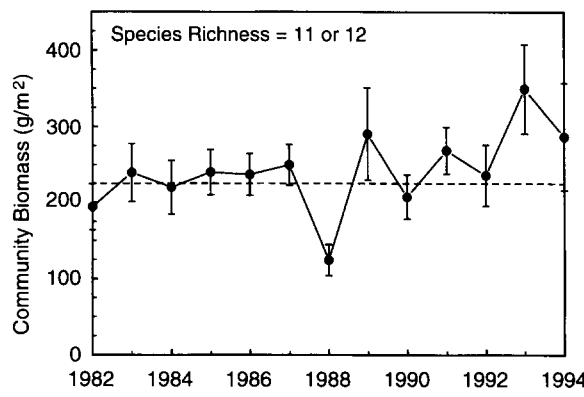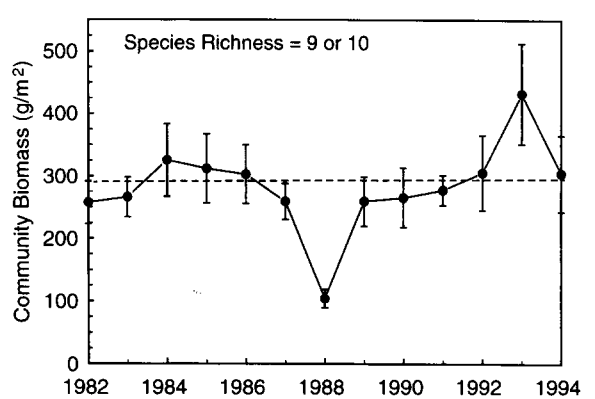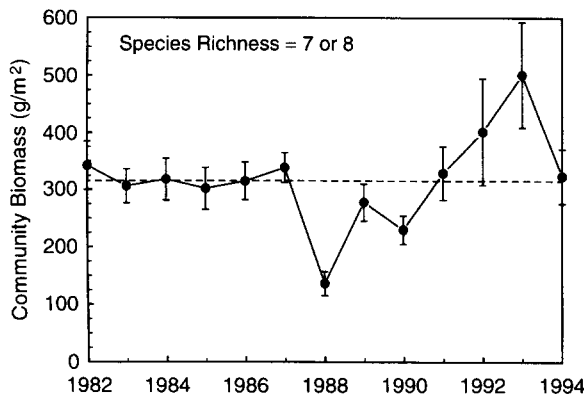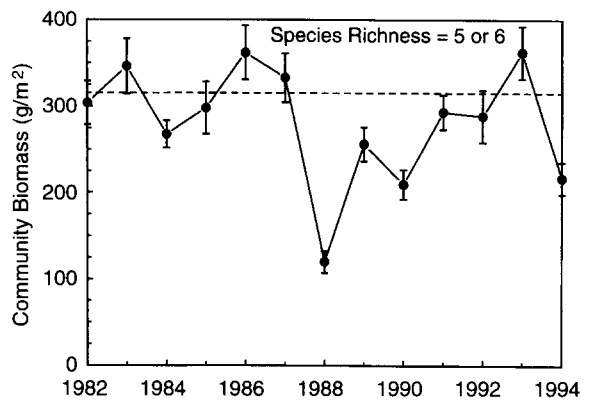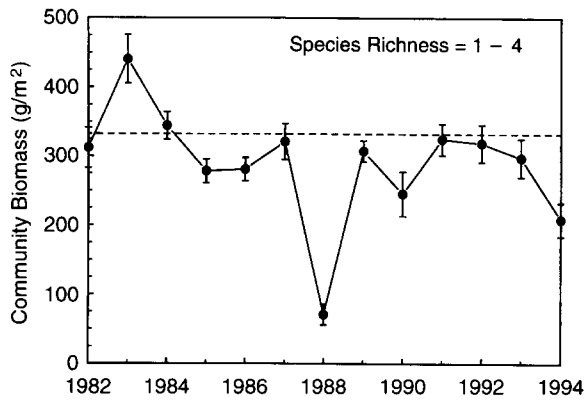
FIG. 5. Proportion of pre-drought biomass that plots attained during drought (biomass$_{1988}$/biomass$_{1986}$), shown on a log scale, is graphed against the 1986 species richness of each plot. Mean ± 1 SE are shown, with the number indicating the number of plots at each level of species richness. RGR is relative growth rate, calculated as the log$_e$ of the biomass ratio divided by 2 (for the 2-yr interval). Modified from Tilman and Downing (1994).
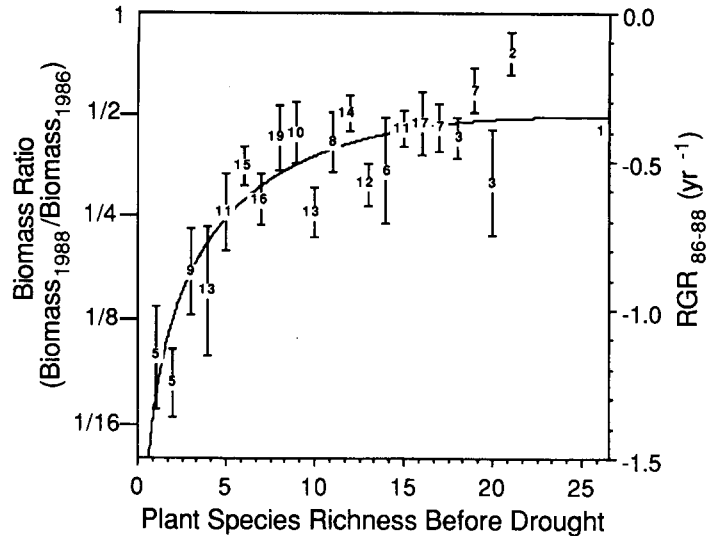
much of the plot-to-plot variation in biomass and species richness resulted from this treatment (Figs. 2 and 3). The biomass of *Schizachyrium,* legume biomass, and log$_e$(community biomass) were significant in all three cases (Tables 1–3), but there was no consistent effect of *Schizachyrium* or legume biomass on stability. Greater *Schizachyrium* and legume biomasses were associated with lower decadal stability (i.e., with greater CV$_{84-94}$ and greater CV$_{ND}$; Tables 2 and 3), but with greater drought resistance (i.e., greater values of RGR$_{86-88}$). Greater log$_e$(community biomass) led to lower stability in all three cases. Because each measure of stability included community biomass in its denominator, even biomass values drawn from a set of random numbers would tend to give a negative correlation between each stability measure and log$_e$(community biomass) (e.g., Eberhardt 1970). However, there were significantly positive correlations (Tables 2 and 3) for the two CVs and log$_e$(community biomass), strongly suggesting that the effect of biomass was not an artifact. The strong negative effect of log$_e$(community biomass) on RGR$_{86-88}$ (Table 1) though, could be at least partly an artifact. To determine if this influenced the relationship between species richness and RGR$_{86-88}$, the multiple regressions that led to Table 1 were repeated but without inclusion of community biomass or log$_e$(community biomass). There remained a significant positive effect of species richness on RGR$_{86-88}$ in both the full model ($F_{1,197} = 8.40$, $P = 0.004$) and that obtained via backwards elimination ($F_{1,197} = 4.03$, $P = 0.04$). As might be expected, the rate of nitrogen addition was retained as a significant variable when community biomass was excluded from analyses.

Drought and species abundances

To categorize the drought response of individual species, the average biomass of a species across all plots before the drought was compared to that during the drought, using (average biomass$_{1988}$)/(average biomass$_{1986}$). If the average biomass of a species was the same before and during the drought, this ratio would be 1. A ratio >1 means that the species increased, on average, during the drought whereas a ratio <1 means that it declined. These were calculated for the 27 most abundant plant species, based on average abundance over all plots for 1984 through 1994, and graphed against their abundance rank (Fig. 8). Many species performed better during the drought than did plant community biomass (shown as the dotted line), and several species increased during the drought.

Species richness and variability in species abundances

All years.—In total, across all plots, there were 729 cases for which a coefficient of variation could be calculated for the biomass of an individual species, given that a species had to occur in a plot for at least 9 of the 11 yr from 1984 through 1994. These 729 cases included 39 different plant species. For these species considered as a group, CV$_{species-ALL}$ was significantly positively correlated with 1984 through 1994 average species richness ($r = 0.15$, $P < 0.01$, $N = 730$; Fig. 9A), but little of the variance in CV$_{species-ALL}$ was explained by species richness. On a species-by-species basis, the five most frequent species in this data set showed differing responses. CV$_{species}$ was significantly ($P < 0.05$)

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FIG. 4. Dynamics of average community biomass (± 1 SE) from 1982 through 1994 for plots grouped by their 1986 plant species richness. For each case, the dashed line is the pre-drought average biomass of the plots (1982 through 1986).

TABLE 1. Multiple regression for the dependence of RGR_{86-88}, the specific rate of change in community biomass from 1986–1988, on other variables as derived by backwards elimination procedure from a multiple regression initially including the 21 candidate variables listed in *Results: Species richness . . . : A. Responses to drought.* The effects listed for Fields A, B, and C indicate that these fields differ significantly in regression intercepts, both one from the other and in comparison with Field D.

A) Analysis of variance

Source	df	Mean square	F value	P
Model	10	2.19	25.6	0.0001
Error	196	0.086		
Total	206			

B) Regression parameter estimates

Variable	Parameter estimate	P	Partial correlation
Intercept	3.31	0.0001	
Log_e[species richness$_{86}$]	0.138	0.0014	0.23
Biomass$_{1986}$ of *Agropyron repens*	0.0022	0.0001	0.35
Biomass$_{1986}$ of *Schizachyrium scoparium*	0.0016	0.0001	0.27
Field A	−0.958	0.0001	−0.55
Field B	−0.26	0.0095	−0.18
Field C	−0.17	0.0245	−0.16
Biomass$_{1986}$ of forbs	0.0012	0.0012	0.23
Biomass$_{1986}$ of legumes	0.0022	0.0018	0.22
Biomass$_{1986}$ of woody plants	0.0011	0.0004	0.25
Log_e[community biomass$_{1986}$]	−0.75	0.0001	−0.58

TABLE 2. Multiple regression of cv_{84-94} (coefficient of variation in community biomass for 1984 through 1994) on other variables derived by backwards elimination from a model that initially contained the 19 candidate variables listed in *Results: Species richness . . . : B. Year-to-year biomass variability and species richness.*

A) Analysis of variance

Source	df	Mean square	F value	P
Model	10	1167.5	15.6	0.0001
Error	194	74.6		
Total	204			

B) Regression parameter estimates

Variable	Parameter estimate	P	Partial correlation
Intercept	−38.8	0.1512	
Species richness$_{84-94}$	−1.89	0.0001	−0.49
Community biomass$_{84-94}$	−0.097	0.0004	−0.25
Biomass$_{84-94}$ of *Schizachyrium*	0.083	0.0012	0.23
Field B	−18.8	0.0001	−0.43
Field C	−10.4	0.0001	−0.37
Biomass$_{1987}$ of root	−0.0067	0.0080	−0.19
Biomass$_{84-94}$ of forbs	0.060	0.0028	0.21
Biomass$_{84-94}$ of legumes	0.113	0.0083	0.19
Biomass$_{84-94}$ of woody plants	0.074	0.0001	0.32
Log_e[community biomass$_{84-94}$]	23.2	0.0002	0.27

positively correlated with SR_{84-94} for *Agropyron repens*, independent of SR_{84-94} for *Panicum oligosanthes* and *Artemisia ludoviciana*, and significantly negatively correlated with SR_{84-94} for *Schizachyrium scoparium* and *Poa pratensis*. When *A. repens* data were deleted from the full data set, the relationship between the $cv_{species-ALL}$ and species richness lost its significance ($r = 0.03$, $N = 630$, $P = 0.4$).

Non-drought years.—Comparable coefficients of variation, but for non-drought years (Fig. 9B), also had a statistically significant positive correlation between species richness and $cv_{species-ND}$ ($r = 0.15$, $N = 441$, $P < 0.01$). The deletion of *A. repens* changed this to a nonsignificant relationship ($r = 0.4$, $N = 365$, $P = 0.50$).

DISCUSSION

This study tests the diversity–stability hypothesis (Elton 1958) by exploring the dependence of community productivity and plant species abundances on plant species richness. Three different measures of community biomass variability were significantly dependent on species richness in a manner that supports the diversity–stability hypothesis. Specifically, based on simple regressions, drought resistance (RGR_{86-88}) was greater in species rich plots, and year-to-year community biomass variability was lower in species rich plots both for the entire 11-yr period and for the nine

non-drought years. This dependence of stability on plant species richness (and on other diversity indices) also held in multiple regressions that controlled for numerous additional variables. Moreover, species richness was retained as a significant variable in simplified multiple regressions obtained by backwards elimination. Thus, community aboveground production in more diverse grassland plots was more stable not only with respect to a rare but major perturbation, drought, but also with respect to more normal year-to-year variation in climate. All additional analyses of these data have shown this also (Tilman and Downing 1994, Tilman et al. 1994, D. Tilman, *unpublished data*). The relationship between drought resistance and species richness (Fig. 5) is remarkably similar to the saturating ("type 2") response of Vitousek and Hooper (1993:6), about which they said, "we anticipate that, in practice, the type 2 pattern will prove to be most widespread in natural ecosystems." In total, the results of this 13-yr study of 207 grassland plots supports the diversity–stability hypothesis.

Species-rich plots returned to their pre-drought biomass more quickly than did species-poor plots (Tilman and Downing 1994), but this does not measure resilience as defined by Pimm (1984) because of the potentially confounding correlation between species richness and the size of the drought effect. When resilience was measured as the proportional return toward pre-disturbance conditions (i.e., relative biomass deviation), simple regression revealed a significant positive
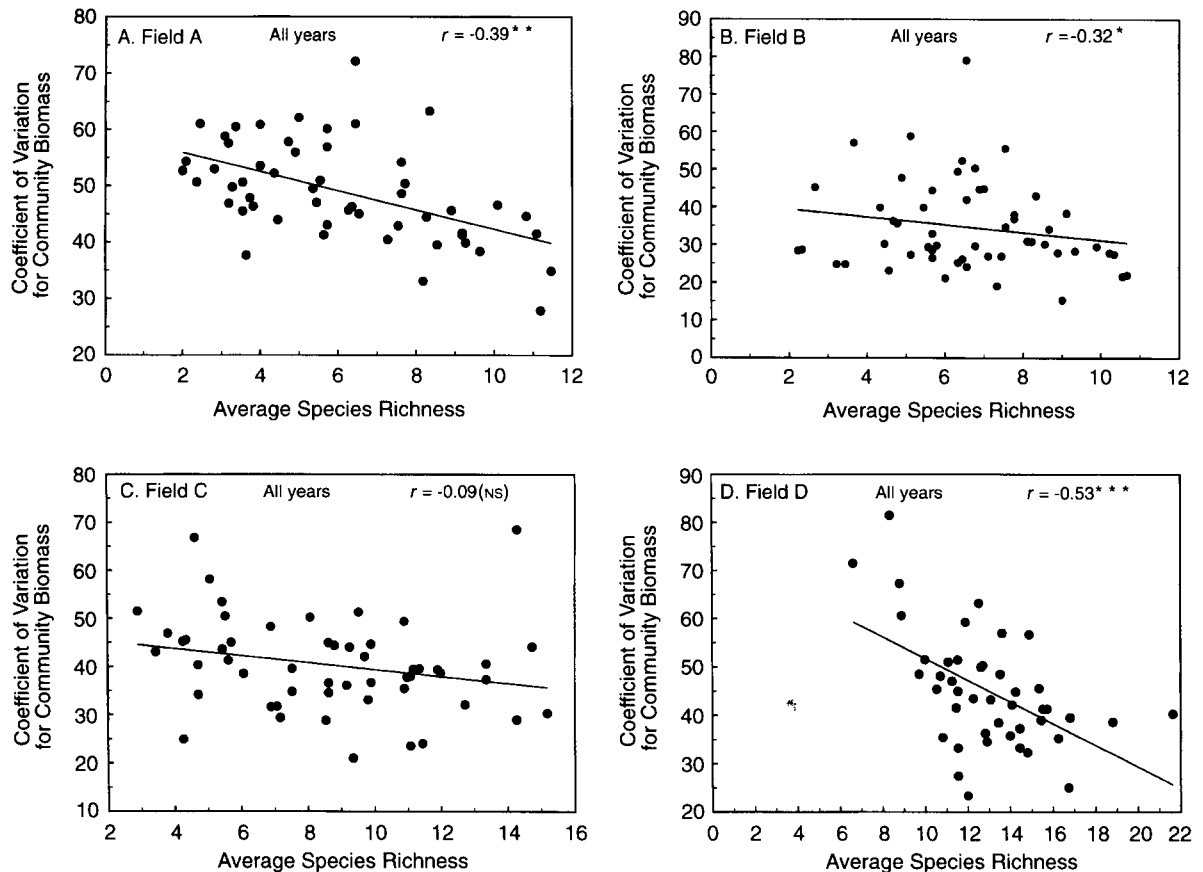
FIG. 6.   Coefficient of variation in community biomass for (A–D) each plot in each of the four fields is graphed against the plot average species richness for this same period (1984 through 1994). Regression lines are shown, as are Pearson correlation coefficients.

effect of species richness on resilience, but this was not sufficiently robust to remain significant in multiple regressions that controlled for potentially confounding variables. Thus, species diversity had a clear and significant effect on resistance to perturbation, but an equivocal effect on the rate of recovery from perturbation.

Although $CV_{species}$ values are not comparable to eigenvalues, both measure dynamic responses to perturbation. In May's (1973) model, communities of competitors were stable (negative eigenvalues) at all levels of species richness, but the dominant eigenvalue became more positive (approached zero) as species richness increased, indicating that perturbations caused species abundances to be more oscillatory and/or less damped in more species-rich communities. The slight, but significantly positive, correlations between the CVs of species biomasses and species richness (Fig. 9) show that, for all species combined, biomasses of individual species tended to have greater year-to-year variability in species-rich plots than in species-poor plots. Although little of the variance in these CVs was explained by the regressions, and they depended on the response

of a dominant species, the overall relationships support May's prediction. This reveals a puzzle: How can the biomass of all species taken together be more stable in more diverse communities, yet the biomasses of individual species be either independent of diversity or less stable in more diverse communities?

The greater stability of community biomass associated with higher diversity would seem to require (1) that species differ in their susceptibility to disturbance and (2) that species compete and thus compensate via competitive release for decreased abundances of disturbance-susceptible species. Such decreases in susceptible species and compensatory increases in other species would cause increased variability in the biomasses of individual species. Cedar Creek plant species have several axes of differentiation (Gleeson and Tilman 1990, McKane et al. 1990, Tilman and Wedin 1991), and show strong interspecific competition (Tilman 1990, Wilson and Tilman 1991a, b, 1993, Wedin and Tilman 1993). It is this competition, and the competitive release that occurred when drought-sensitive plants were harmed by drought, that may explain the increased growth of some species during the drought
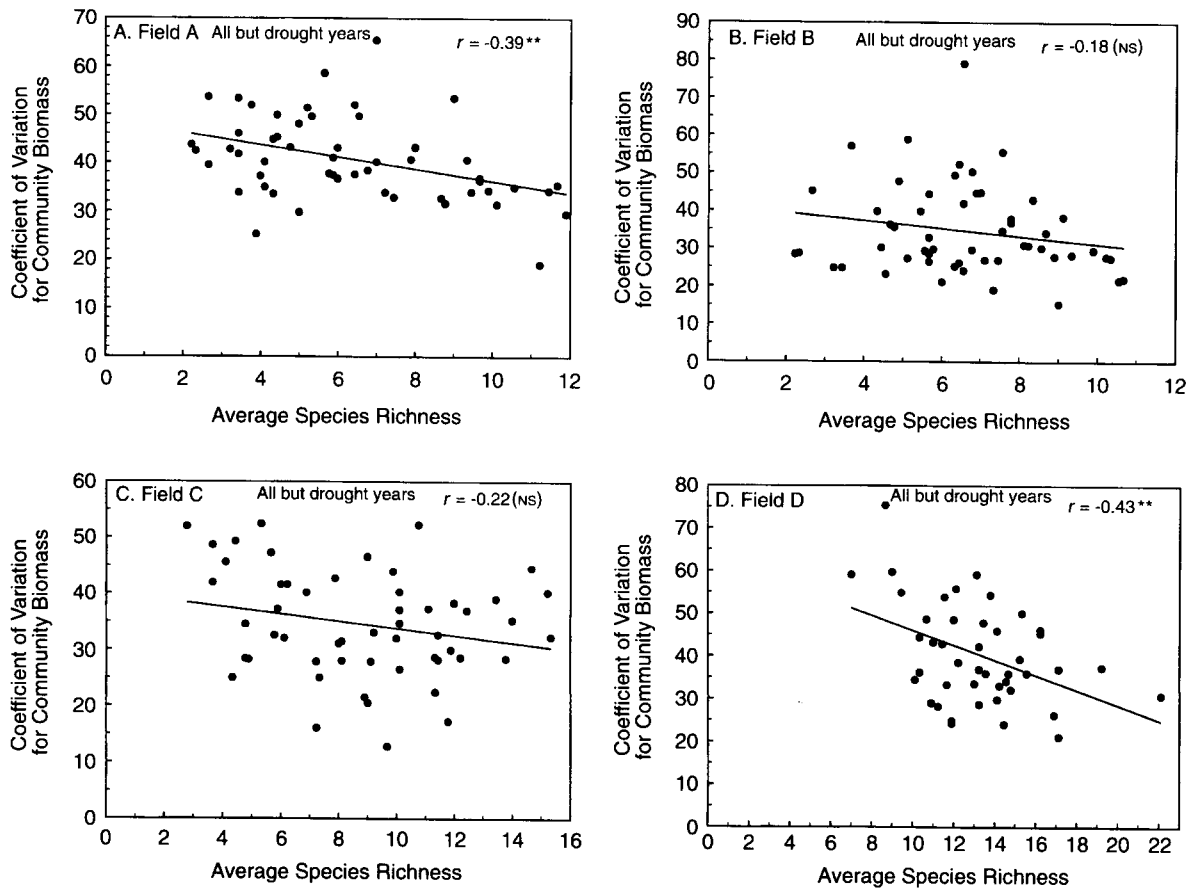
FIG. 7. Coefficient of variation in community biomass for non-drought years (1984 through 1986 and 1989 through 1994), presented as in Fig. 6.

(Fig. 8). If this is correct, the magnitude of the increase in the biomass of the increasing species should be dependent on the extent to which the abundances of other species declined during the drought. To test this hypothesis, I calculated the change in the summed abundance of four major increasing species (*Sorghastrum nutans, Andropogon gerardi, Asclepias syriaca,* and *Asclepias tuberosa*; Fig. 8) and compared it to the change in the community biomass of all other species in each plot in which they occurred. There was a significant negative correlation between these two variables ($r = -0.29$, $P < 0.01$, $N = 72$), indicating that greater decreases in the biomass of other species led to greater increases in the abundances of the increasing species. This supports the hypothesis of compensatory growth caused by competitive release.

Given interspecific competition and differential susceptibility to disturbance, does species richness necessarily stabilize community biomass? Consider a simple case—a community consisting of just two competitors. Let species A be disturbance resistant and species B be disturbance sensitive. Assume that, during normal years, each species has a biomass of K in mono-

culture and of $K/2$ in two-species mixtures. Thus, before disturbance, the average biomass of both monocultures and mixtures would be K. During a disturbance, species A would still attain a biomass of K in monoculture (being disturbance resistant), whereas species B would have a biomass of 0. During a disturbance the average biomass of monocultures would decrease to $(K + 0)/2$, or $K/2$, which is one-half of the average during normal years. All that is required for the two-species mixtures to have a greater average biomass during disturbance is for species A, which is disturbance resistant, to increase in abundance in the mixture plots in which species B has died. If it can increase by an amount C because of competitive release, the average biomass of mixtures during disturbance would be $(K + C)/2$, which is clearly greater than $K/2$. If species A could completely compensate for the loss of B, mixtures would have average community biomass of K during disturbance.

Although the mathematics get messier, this logic can be dressed up in the fancier clothing of Lotka-Volterra, resource, or other competition models, and gives similar results. If some species are harmed to any extent

TABLE 3. Multiple regression of CV_{ND} (non-drought years) on other variables, as derived by backwards elimination from a model initially containing 19 candidate variables comparable to those used for Table 2, but based on data for non-drought years.

A) Analysis of variance

Source	df	Mean square	F value	P
Model	10	803.0	9.9	0.0001
Error	194	81.5		
Total	204			

B) Regression parameter estimates

Variable	Parameter estimate	P	Partial correlation
Intercept	3.13	0.7487	
Species richness$_{ND}$	−1.58	0.0001	−0.31
Biomass$_{ND}$ of *Agropyron repens*	0.161	0.0044	0.20
Biomass$_{ND}$ of *Schizachyrium scoparium*	0.082	0.0052	0.20
Biomass$_{ND}$ of *Poa pratensis*	0.154	0.0092	0.19
Field B	−16.4	0.0001	−0.36
Field C	−8.57	0.0010	−0.23
Biomass$_{1987}$ of root	−0.0065	0.0125	−0.18
Biomass$_{ND}$ of C_3 grasses	−0.196	0.0006	−0.24
Biomass$_{ND}$ of legumes	0.087	0.0347	0.15
Log$_e$[community biomass$_{ND}$]	11.0	0.0001	0.38

by a disturbance and others are not, the average response of monocultures is just the average of the individual responses. However, in mixtures, the average includes compensatory growth produced by disturbance-resistant species because of decreased competition. This compensatory growth causes mixtures to outperform monocultures. Because plots with greater species richness should have a higher probability of containing more disturbance-resistant species, high-di-

versity mixtures, on average, should outperform low-diversity ones.

Similar processes seemed to have operated in McNaughton's (1977) study of grazing in the Serengeti. Plots with greater plant species richness were more likely to contain some grazing-resistant plant species, the growth of which allowed these to more rapidly re-attain their pre-grazing community biomass. McNaughton summarized this as "species diversity mediates community functional stability through compensating interactions to environmental fluctuations among co-occurring species" (McNaughton 1977:523).

In total, the results reported here, and those of McNaughton (1977), Lepš et al. (1982), and Frank and McNaughton (1991) have shown that greater plant species diversity led to greater stability of plant community biomass after a perturbation. This supports the hypothesis that diversity stabilizes community and ecosystem properties. My results have also shown that higher plant diversity is weakly associated with lower stability of abundances of individual plant species, as hypothesized by May (1973). The mechanism that unifies these seemingly different results is interspecific competition. Interspecific competition can magnify the effects of a perturbation on the abundances of individual species because a change in the abundance of one species will impact the abundances of many others in the competitive network. However, competition also constrains community biomass, and the competitive release experienced by disturbance-resistant species acts to stabilize community biomass in species rich communities. This resolution was predicted by King and Pimm (1983) and foreshadowed in Robert May's (1974: 231–232) "Afterthoughts" to his 1973 book:

if we concentrate on any one particular species our impression will be one of flux and hazard, but if we

FIG. 8. Change in the average biomass of 24 abundant species, from before the drought (1986) to the peak of the drought (1988), graphed against their ranked abundance. Calculations were performed for the 27 most abundant species, but species that were absent in one of the two years are not shown. The dashed line shows the response of community biomass. Each dot represents a species. Number codes, presented in order of occurrence in the figure, identify each species, with 100 = *Agropyron repens*, 117 = *Poa pratensis*, 103 = *Schizachyrium scoparium*, 508 = *Artemisia ludoviciana*, 305 = *Rubus* sp., 120 = *Sorghastrum nutans*, 200 = *Carex* sp., 303 = *Rhus glabra*, 402 = *Lathyrus venosus*, 502 = *Ambrosia coronopifolia*, 304 = *Rosa arkansana*, 102 = *Andropogon gerardi*, 562 = *Solidago rigida*, 604 = *Solidago graminifolia*, 111 = *Panicum oligosanthes*, 509 = *Asclepias syriaca*, 512 = *Aster azureus*, 125 = *Calamagrostis canadensis*, 510 = *Asclepias tuberosa*, 122 = *Stipa spartea*, 513 = *Berteroa incana*, 231 = *Cyperus* sp., 561 = *Solidago nemoralis*, 403 = *Lespedeza capitata*.
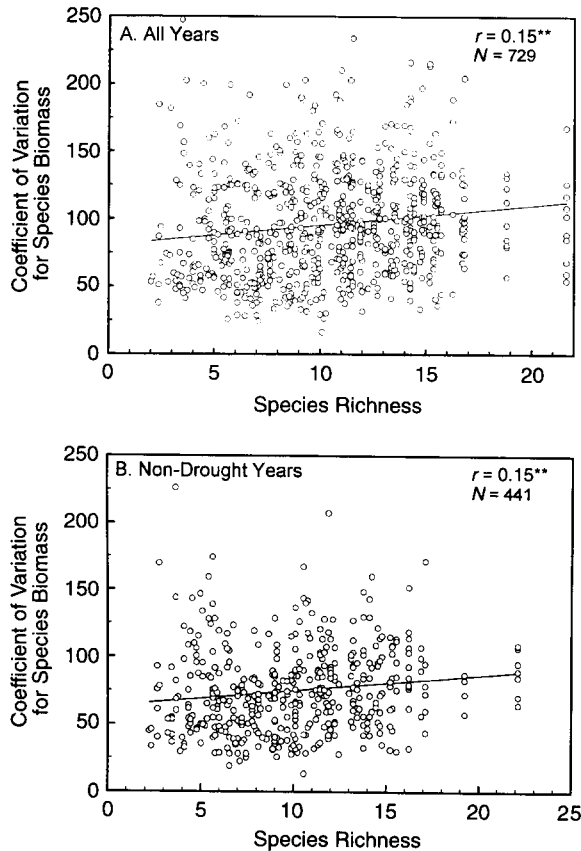
DAVID TILMAN
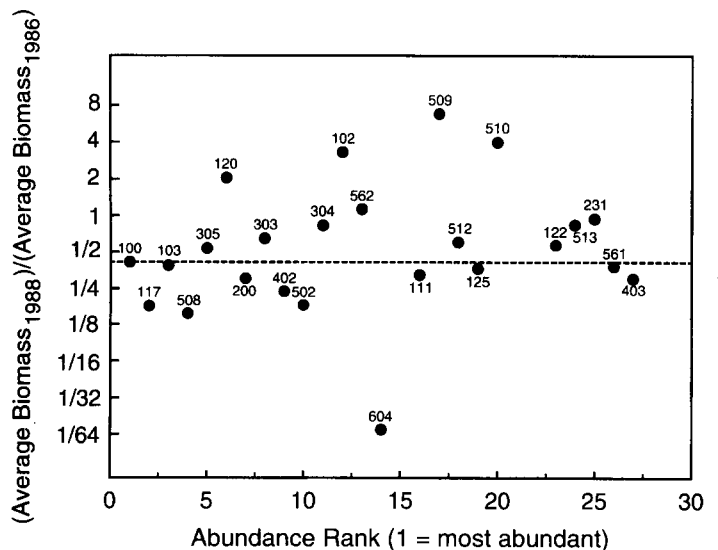
FIG. 9. (A) Coefficients of variation for year-to-year variation in biomass of individual species in a plot, graphed against average species richness of the plot in which a species occurred, using data for all years from 1984 through 1994. The graph shows results for all 39 common species combined; (B) a similar graph, but showing results for all non-drought years (1984 through 1994, but not 1987 or 1988). Lines shown are linear regressions. Pearson correlation coefficients are given.

concentrate on total community properties (such as biomass in a given trophic level) our impression will be of pattern and steadiness.

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