

Drought and biodiversity in Grasslands

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Received December 18, 1990 / Accepted in revised form September 2, 1991

Summary. The local species richness of four different grassland fields fell an average of 37% during a 1988 drought that decreased above-ground living plant mass by an average of 47%. Despite the return to more normal plant mass and precipitation during the next two years, there was no significant recovery in species richness in the 46 permanent plots, suggesting that local species richness became recruitment limited. The drought led to the loss of annual species independent of their abundance. For perennial grasses, perennial forbs, legumes and woody species, the probability of a species being lost from a plot was significantly negatively correlated with its pre-drought abundance. These results demonstrate that environmentally extreme conditions can limit species richness by causing the local extinction of rare species. Because droughts of this intensity occur about every 50 years in the prairie, periodic drought may have limited prairie diversity. Moreover, if the accumulation of greenhouse gases leads to a more variable or extreme climate, it could cause increased rates of species extinctions.

Key words: Drought – Extinctions – Species richness – Diversity – Colonization

The number of species in a habitat should represent a balance between forces that allow species to invade and persist and forces that drive species to local extinction (e.g., MacArthur and Wilson 1967). Numerous factors, especially spatial heterogeneity, trophic complexity, localized disturbance, colonization strategies, and resource fluctuations, can be important in allowing species to persist (e.g., Grubb 1977; Grime 1979; Lubchenco 1978; Connell 1978; Huston 1980; Armstrong and McGehee 1980; Silvertown 1980; Tilman 1982; Begon et al. 1986).

Indeed, such factors can, in theory, allow an almost unlimited number of species to coexist (Tilman 1982, pp. 234–268). One of the forces that has been suggested as limiting species richness is environmental variability (e.g., Wallace 1878, May 1973, Levinton 1979, Hubbell 1979). Climatically extreme conditions, such as droughts, may periodically lower population densities and thus increase the probability of extinction for rare species. If all else were equal, habitats that experienced greater environmental fluctuations would have greater extinction rates, and thus lower species richness, than more stable habitats (Levinton 1979).

Furthermore, rapid global climatic change may be occurring, and may impact the biodiversity of otherwise undisturbed environments. Although there are data on local colonization and extinction rates for a range of taxa (e.g., Simberloff 1976; Lynch and Johnson 1974; Nilsson and Nilsson 1982, 1985; Robinson and Quinn 1988), few studies are of sufficient duration to document the effects of environmental variation. During the past nine years (1982–1990), we have gathered data annually on species composition, abundance, and richness in 46 grassland plots. These plots are the experimental controls for a study of the effects of nitrogen supply rate on the composition, dynamics, and diversity of successional grasslands and prairie remnants in Minnesota (Tilman 1987, 1988). Because our study period included the most severe regional drought of the past 50 years (Fig. 1), as well as periods of more normal precipitation, we decided to determine if drought had a significant effect on species richness and on rates of species loss and gain in these plots. Simple models of random walk to extinction often assume that rarity should be the most important determinant of the probability of local extinction (e.g., May 1973, Hubbell 1979). Alternatively, species may differ in their susceptibility to loss by drought. Thus we also determined how the probability of a plant species being lost from a plot during the drought depended on its life history, life form, and abundance.

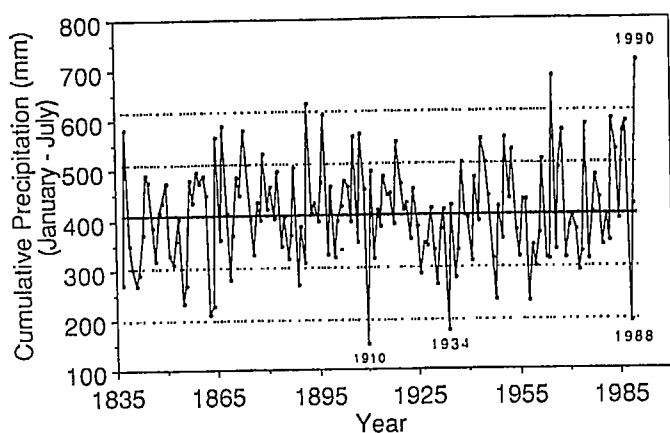


Fig. 1. Growing season cumulative precipitation (January through July) for each year from 1836 to 1990 for the Fort Snelling weather station, (now the Minneapolis-St. Paul International Airport weather station). This station is located approximately 40 miles south of Cedar Creek Natural History Area. The thick, solid line shows mean precipitation for this period, and the other finer lines show one and two standard deviations from the mean

Methods

Data on species richness come from control plots in an experiment described in Tilman (1987). We briefly summarize methods here. The plots were located on the existing vegetation of four upland fields at Cedar Creek Natural History Area (CCNHA), Minnesota. All were on the Anoka sandplain which contained a mosaic of prairie, oak savannah, and oak woodland before farming (Tilman 1987). Fields A, B and C had been abandoned from farming 14, 25 and 48 year, respectively, when this work began in 1982. These fields have never been burned since abandonment. The plots in Field D were in a native prairie opening in a stand of oak savanna that had never been farmed or clearcut, and which has been maintained as savannah by burning for two out of each three years for the past 26 years (Tester 1989). All fields contained grassland vegetation. The younger fields were dominated by European pasture grasses and the older fields by native prairie species (Inouye et al. 1987). Woody plants were rare. None of the plots have ever been watered. All were fenced in 1982 to exclude mammalian herbivores.

We report, here, results for two different types of control plots, called treatments A and I. Treatment I plots received no nutrients of any sort, whereas treatment A plots received annually all nutrients except nitrogen (i.e., P, K, Ca, Mg, S, Co, Mo, B, Zn, and Cu; amounts in Tilman 1987), beginning in 1982. There were 6 replicate 4 m × 4 m plots per treatment in Fields A, B and C, and 5 replicate 4 m × 2 m plots per treatment in Field D. A completely randomized experimental design was used within each field.

Plant abundances were determined annually by clipping a 10 cm × 300 cm strip of vegetation in each plot. Each field was sampled on approximately the same date each summer (Tilman 1987). A different portion of each plot was clipped each year. Each clipped sample was sorted to species, dried and weighed. A working herbarium with voucher specimens, and continuity in personnel, assured consistent species identifications. The species richness of a given treatment was calculated on three different spatial scales. Species richness per plot is the total number of vascular plant species in an individual 0.3 m² sample clipped from a plot in a given year. Species richness per field is the number of vascular plant species found, in total, in all replicates, combined, of a treatment in a given field and year. Total species richness is the total number of vascular plant species observed across all fields for the 23 plots of a treatment combined into a single sample each year. The progression from species richness per plot to species richness per field to total species richness represents the species pool of an increasingly larger set of samples spread over a larger geographic region.

Each, though, includes only the species within a particular treatment.

Species richness data were compared with two different measures of climate and water availability that were calculated using data from the Cedar weather station (note that Fig. 1 used the much longer data record from the Minneapolis weather station). Cumulative precipitation is the cumulative total precipitation occurring from January 1 through July 31 of each year. We included precipitation from January to March because snow is an important source of early growing season moisture. We excluded data after July because we had sampled most plots by the end of July, and precipitation after this date could not affect the results for that year. The relative rainfall deficit was calculated by summing, over this same period, the difference between monthly potential evapotranspiration (calculated using Thornthwaite's formulas) and monthly precipitation. This sum was then divided by the cumulative potential evapotranspiration for that same period. This index includes effects of both precipitation and temperature, with negative numbers indicating rainfall in excess of potential evapotranspiration.

Pearson correlations, regressions, contingency tables, analyses of variance (ANOVA), and contrasts between treatment means (based on Duncan's Multiple Range Test) were performed on a Sun Sparc computer using SAS software (Release 6.03), including the SAS General Linear Models Procedure.

Results

The overall ANOVA of species richness per plot with treatment (A and I), field (A, B, C and D), and year (1982–1990) as factors was highly significant (Table 1). Field and year effects were highly significant, but treatment effects were not (Table 1). The field × year and the field × treatment interactions were significant but other interactions were not. The fields differed in mean species richness per plot (Field A: 9.0 species per plot; Field B: 9.2; Field C: 13.4; Field D: 14.7). There were no significant differences between Treatments A and I in either total biomass or species richness per plot ($P > 0.05$ for both Duncan's contrasts).

Because of the significant two-way interactions, contrasts of species richness in different years of the experiment are best performed separately for each field. However, because neither the treatment effect nor the treatment × year interaction were significant, treatments A and I can be combined in these contrasts of years

Table 1. *F*-values for an analysis of variance of species richness per plot, using data from the four fields, for each year (1982 through 1990) and treatment (A and I). The overall $r^2 = 0.63$ with 341 degrees of freedom for error. The general linear models approach of SAS was used, with *F*-values based on Type III sums of squares

Source	D.F.	<i>F</i> -value
Overall Model	71	8.14 ***
Factors:		
Field	3	85.6 ***
Year	8	29.1 ***
Treatment	1	0.69 NS
Field × Treatment	3	4.87 **
Field × Year	24	1.90 **
Year × Treatment	8	0.76 NS
Field × Year × Treatment	2	0.87 NS

NS means $P > 0.05$; * means $0.05 \geq P > 0.01$; ** means $0.01 \geq P > 0.001$; *** means $P < 0.001$

Table 2. Average species richness per plot for treatments A and I combined for each year of the experiment in each field. Means within a field that share the same lower-case letter do not differ significantly ($P > 0.05$; Duncan's Multiple Range Test). Comparisons were made within each field, but not among fields. The F-value for an ANOVA of species richness by year is shown for each field. All are significant at $P < 0.01$. There were 8 and 99 degrees of freedom for all ANOVA's except that for Field D, which had 8 and 80 degrees of freedom

Year	Field A	Field B	Field C	Field D
1982	11.92 ^b	10.00 ^{ab}	12.42 ^{abcd}	14.50 ^{bc}
1983	12.67 ^{ab}	9.50 ^{ab}	13.75 ^{ab}	15.60 ^{ab}
1984	14.58 ^a	11.08 ^a	13.83 ^a	17.40 ^{ab}
1985	10.75 ^{bc}	9.17 ^{abc}	12.75 ^{abc}	15.30 ^{ab}
1986	14.50 ^a	9.50 ^{ab}	14.08 ^a	18.10 ^a
1987	9.42 ^c	8.33 ^{bcd}	12.42 ^{abcd}	16.70 ^{ab}
1988	5.25 ^d	6.25 ^d	10.83 ^{cd}	10.70 ^d
1989	6.25 ^d	6.25 ^d	9.92 ^d	11.60 ^d
1990	7.08 ^d	7.00 ^{cd}	11.08 ^{bcd}	12.22 ^{cd}
ANOVA				
F-value	19.82	4.86	2.89	7.73

(Table 2). Species richness in 1988, 1989, and 1990 did not differ significantly within any field, but, within each field, it was lower than in most pre-drought years.

Compared to the other years of this study, cumulative precipitation was at its lowest (Fig. 2A) and relative rainfall deficit was at its highest (Fig. 2B) in 1988. The drought began in 1987, had its greatest intensity in 1988, declined in 1989, and had clearly ended by 1990, which was the wettest of the 9 years. Above-ground biomass provides a measure of the intensity of the drought. For each field, and on average across all fields (Fig. 2C), total above-ground biomass declined significantly from 1987 to 1988 but recovered in 1989.

The simplest way to explore the effects of the drought on species richness is to combine the species richness data from the four fields. However, because of the highly significant field \times treatment interaction (Table 1), it is necessary to consider Treatments A and I separately. Separate ANOVA's for Treatments A and I revealed highly significant field and year effects for each treatment ($P < 0.001$), but no significant field \times year interaction for Treatment A ($F_{24,170} = 1.19$, $P = 0.25$), and a weak field \times year interaction for Treatment I ($F_{24,171} = 1.62$, $P = 0.04$). Thus, it is an acceptable approximation to average over fields and calculate the average species richness in each treatment each year. This data lumping allows an easier exploration of the effects of climate on species richness.

Average species richness per plot for Treatments A or I was fairly constant from 1982 to 1986, but had declined dramatically by 1988 (Fig. 3A). Average species richness per plot did not recover significantly in 1989 or 1990. Contrasts of means using Duncan's Multiple Range Test showed that species richness per plot for both Treatments A and I was significantly ($P < 0.05$) lower in 1988, 1989 and 1990 than in any of the preceding years. The same pattern occurred when each field was considered individually (Table 2). Average species richness per field

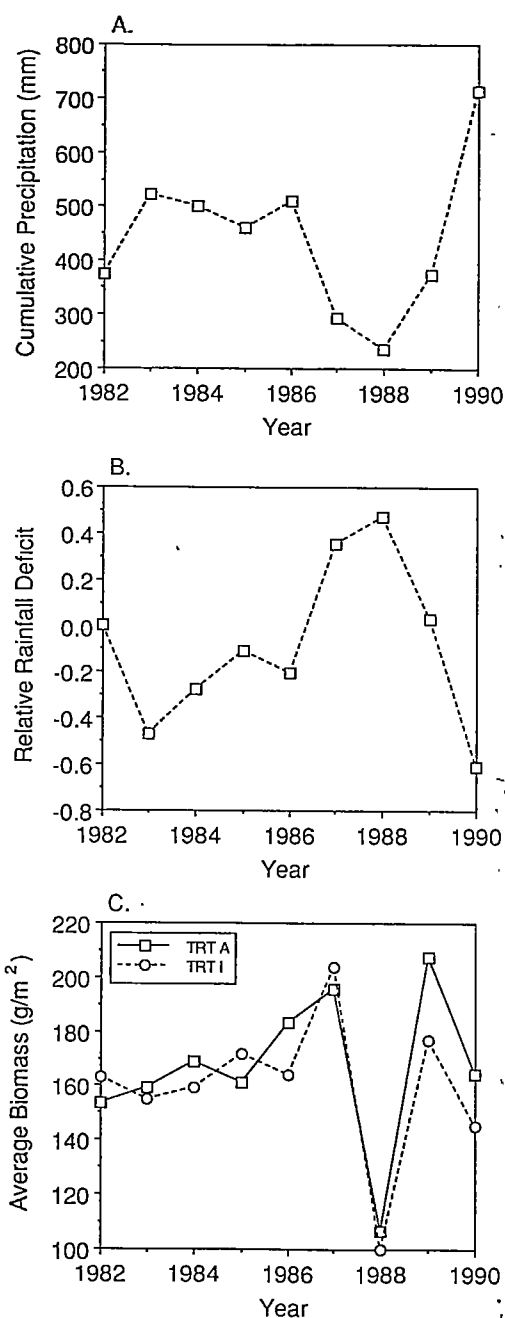


Fig. 2. A, B Cumulative growing season precipitation (January through July) and the calculated relative rainfall deficit for 1982–1990, based on data collected at the Cedar weather station, 4 miles from CCNHA. C Average above-ground living plant biomass in the four fields for either the unfertilized plots (Treatment I) or the plots receiving all nutrients except N (Treatment A). Note that none of the graphs has its origin at zero

and total species richness were also lower in 1988, 1989 and 1990 than in previous years (Fig. 3B and C), with a suggestion of total species richness increasing from 1988 to 1990.

For the period from 1982 through 1988, species richness per plot for Treatment A (averaged over all four fields) was significantly positively correlated with cumulative precipitation (Fig. 4). In contrast, it was independent of precipitation for the period from 1988 to 1990

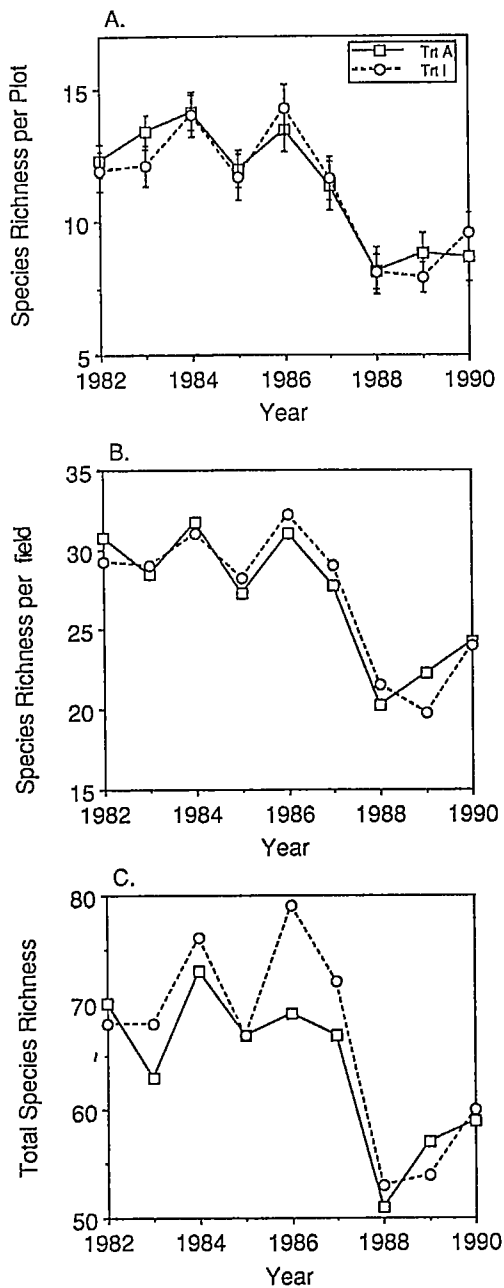


Fig. 3. A. Species richness per plot, averaged over the four fields, is graphed against year, with treatment A (all nutrients except N) and treatment I (no nutrient addition) shown separately. Standard errors are shown. B. Species richness per field, averaged over the four fields, is graphed against year. C. Total species richness, i.e., the total number of species in a combined sample of all replicates of a treatment in all four fields, is graphed against year.

(Fig. 4). Average species richness per plot in Treatment I had similar patterns for the pre-drought and post-drought periods (Fig. 4). For all fields, 1989 and 1990 species richness per plot were significantly lower than in other years with comparable precipitation. Similar patterns occurred when species richness per plot results were graphed against relative rainfall deficit. This is to be expected because cumulative precipitation and the index of relative rainfall deficit were highly significantly correlated ($r = -0.96$, $n = 9$, $P < 0.01$). Patterns similar to,

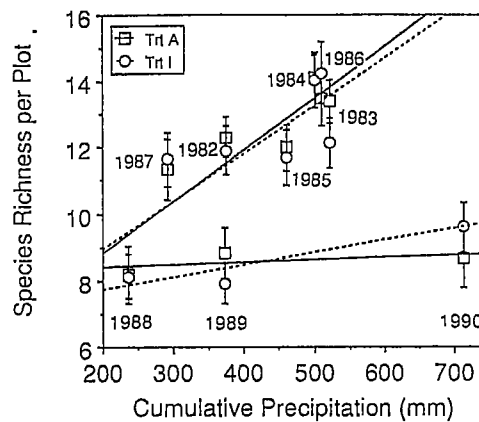


Fig. 4. Species richness per plot, averaged over the four fields, is graphed against the cumulative precipitation of each year of the study. Data for both treatments A and I are shown. The solid line with a steep slope is a regression of 1982 through 1988 data for treatment A. The comparable regression for treatment I has a broken line. Regressions of species richness versus cumulative precipitation for 1988 through 1990 are also shown, and neither has a significant slope.

but not as strong as, those in Figure 4 occurred when the other two measures of species richness were graphed against precipitation.

Because of the major change in species richness between 1986 and 1988, we compared the species composition of plots, on a plot-by-plot basis, to determine how many vascular plant species had been lost, gained, or remained present ("unchanged") from 1986 to 1988. We also classified these plants by life form and reproductive mode. We then compared annuals with perennials (which did not include biennials) and compared grasses with forbs (which did not include legumes). We averaged these over all plots of a treatment in each of the four fields (Table 3). Because we subsampled vegetation each year, there is sampling error in each census (Nilsson and Nilsson 1982, 1985). Thus, part of the turnover in species composition is sampling noise, which Nilsson and Nilsson (1985) have called "pseudoturnover". However, because we expended the same sampling effort and used identical sampling methods in each plot each year, we can still determine if the drought was associated with changes in the turnover rates of various taxa.

On average across the four fields, 96% of the annual species that had been present in 1986 were absent from the plots in 1988. The number of new annual species appearing per plot was, on average, only 6% of the total number of annual species present in 1986. On average, 47% of the perennials originally present in a plot were lost from 1986 to 1988, but new perennial species appearing in an average plot were 22% of the 1986 perennial species richness. Across all four fields, an average of 6.0 forb species were lost per plot from 1986 to 1988, which represented 76% of the forbs present in 1986. There were 1.6 species of grasses lost per plot, which comprised 36% of the grasses present in 1986, on average. New forb and grass species were about equally likely to be gained in 1988, with a gain, on average, of 19% new species for forbs per plot and 14% for grasses (Table 3).

Treatment I

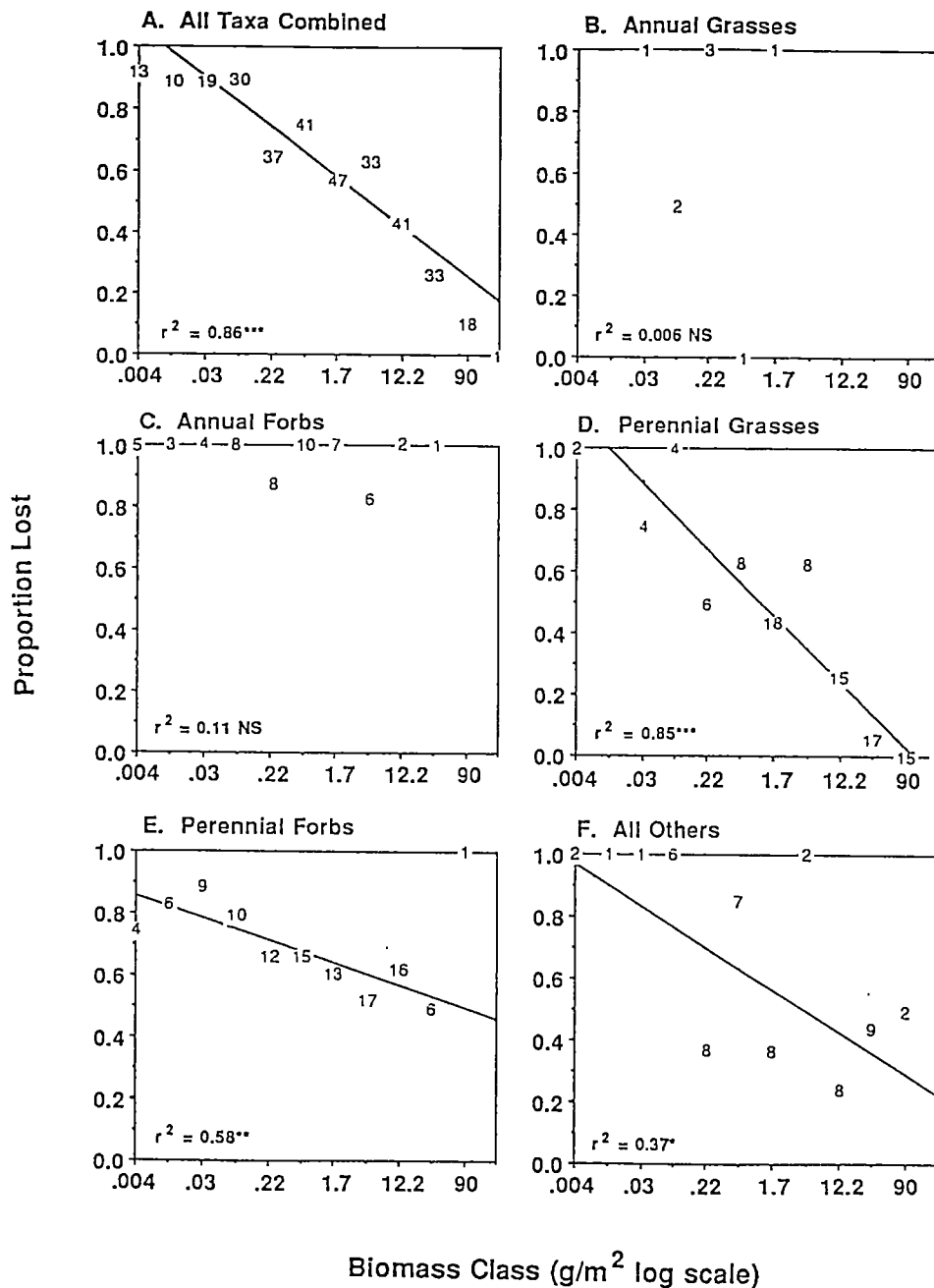


Fig. 5A-F. For all Treatment I plots combined, each species present in a given plot was assigned to one of 12 biomass classes based on its 1986 biomass in that plot, and assigned to a plant life form class. The total number of entries in each class is indicated by the numbers in each figure. A loss occurred if a species was present in a plot in 1986 but absent in 1988. The proportion of species lost within each class is graphed against the abundance of that class, for six different classes of plants

During the drought, the species most commonly lost in Field A were the annual forbs *Erigeron canadensis*, *Ambrosia artemisiifolia*, and *Hedeoma hispida* and the perennial grass *Agrostis scabra*. For Field B, the most commonly lost species were the perennial sedge *Cyperus filiculmis*, *Agrostis scabra*, the annual grass *Aristida basiramea* and numerous rare annual forbs. For Field C, *Aster azures* and *Liatris aspera*, both perennial forbs, *Agrostis scabra*, *Hedeoma hispida*, and *Cyperus filiculmis* were the species most frequently lost. In native prairie (Field D), the two most commonly lost species were both native prairie perennial forbs, *Liatris aspera* and *Solidago graminifolia*. Other Field D species lost included the

legume *Vicia villosa*, the perennial forbs *Anemone cylindrica*, *Potentilla recta*, and *Ambrosia coronopifolia*, and the annual grass *Aristida basiramea*.

Each species present in a plot in 1986 was assigned to one of 12 abundance classes (log scale) based on its 1986 biomass (g/m²), classified as to whether it was lost (absent from that plot in 1988) or not lost (present in that plot in 1988), and assigned to one of five classes based on life form and reproductive mode (annual grass, annual forb, perennial grass, perennial forb, or other, where other consisted of legumes, biennials, and woody species). Data from all four fields and all abundance classes were combined to create a contingency table that com-

Treatment A

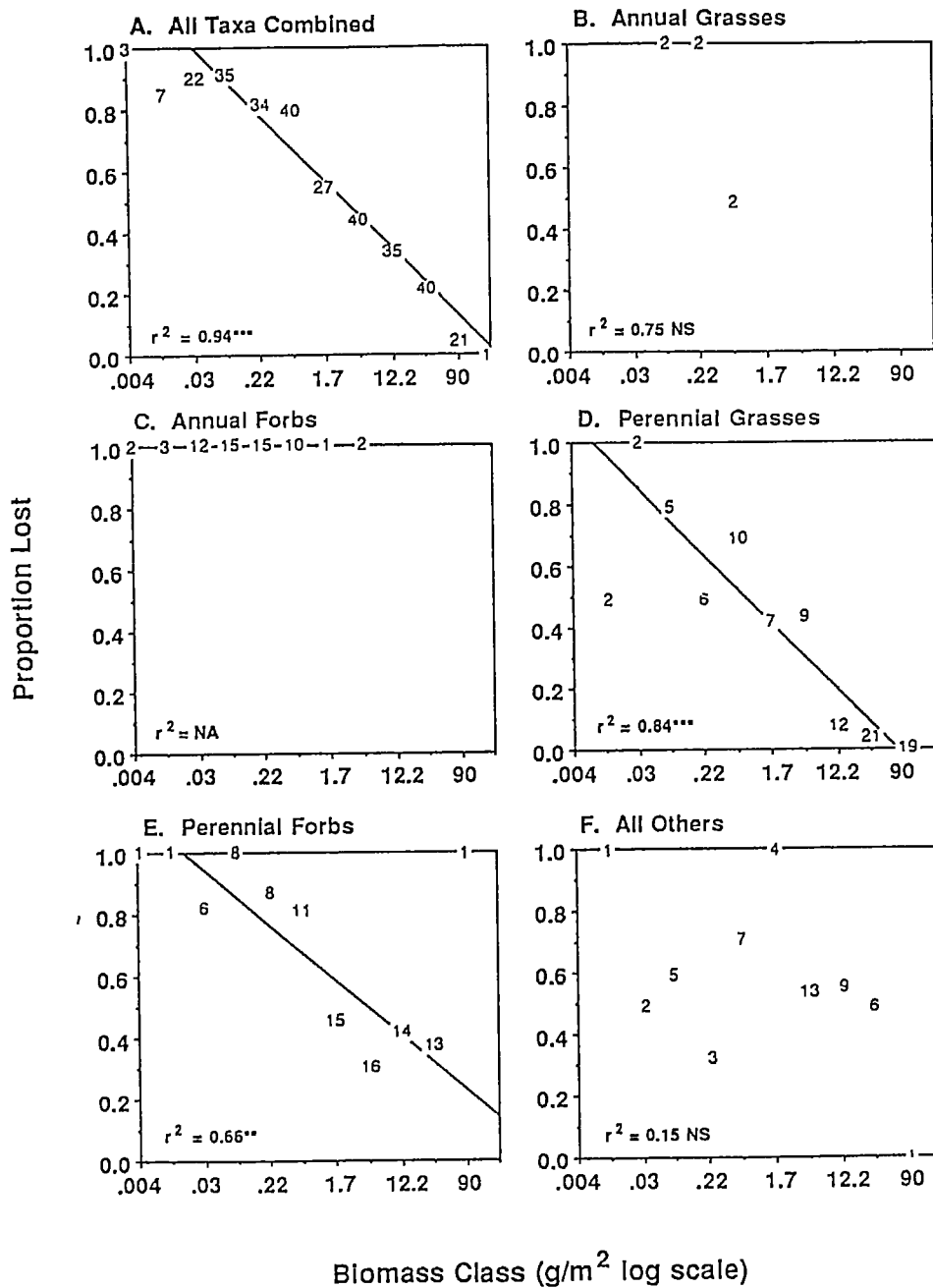


Fig. 6A-F. Identical to Figure 5, except that data are from Treatment A plots

pared the number of species in each of the five life form classes that were either lost or not lost. This revealed that the five life form classes differed significantly in the proportion of species that were lost during the drought ($X^2 = 134.5$, d.f. = 4, $p < 0.001$).

We also calculated the proportion of species in each abundance class and life form class that were lost from 1986 to 1988 (Figs. 5 and 6). For these analyses, we combined data from all four fields, but analyzed Treatments A and I separately. For both annual forbs and

annual grasses, there was no correlation between the proportion of species lost and the 1986 abundance of the species for either Treatment A or I. In contrast, for perennial forbs and for perennial grasses, the probability that a species would be lost from 1986 to 1988 increased significantly with its rarity for both Treatments I and A (Figs. 5 and 6). All other taxa (mainly legumes) also were more likely to be lost the rarer they were in Treatment I, but did not show this pattern in Treatment A. When data for all taxa were combined (Fig. 5A and 6A), the

Table 3. The number of species per plot that were either lost from 1986 to 1988, that were gained between 1986 and 1988, or that were present in a plot in both 1986 and 1988 ("unchanged"), as calculated on a plot-by-plot basis. Results shown are per-plot averages over

all replicates of a treatment in a given field. Results are shown for all vascular plant species combined and for two subgroups (annuals vs. perennials; forbs vs. grasses)

Field	Trt	All vascular plant species			Annuals			Perennials			Forbs			Grasses		
		Lost	Gained	Un-changed	Lost	Gained	Un-changed	Lost	Gained	Un-changed	Lost	Gained	Un-changed	Lost	Gained	Un-changed
A	A	10.3	2.0	4.2	5.7	0	0	2.8	2.0	2.0	8.5	0.8	0.3	1.5	1.0	1.8
A	I	12.5	2.2	6.0	7.3	0	0.3	4.5	2.2	2.5	10.0	1.3	1.5	2.0	0.7	2.3
B	A	6.2	1.8	6.3	3.7	0.2	0.2	2.2	1.5	4.2	5.0	0.8	1.0	1.0	0.7	3.0
B	I	3.5	1.2	7.0	1.2	0	0.2	1.8	1.0	4.7	1.8	1.2	1.8	1.0	0	2.5
C	A	6.3	3.7	9.3	0.8	0.2	0	4.3	3.2	7.3	4.5	2.0	3.3	1.0	0.8	3.3
C	I	7.7	3.8	8.8	0.3	0.2	0.2	6.2	3.7	6.7	5.5	2.0	3.3	1.0	1.2	3.2
D	A	9.2	2.8	10.0	0.8	0.2	0	8.0	1.4	9.0	5.4	2.4	2.6	2.0	0	3.8
D	I	12.4	3.4	7.2	1.4	0.8	0	10.2	2.6	6.2	7.2	1.6	1.4	3.4	0.6	3.4

probability of a species being lost increased highly significantly with its pre-drought rarity for both Treatments A and I. This selective loss of rare species during the drought truncated dominance-diversity curves, giving them a less linear (geometric) but more sigmoidal (log normal) shape.

Discussion

A drought as severe as that of 1988 has occurred about once every 50 years in Minnesota (Fig. 1). The 1988 drought caused the local extinction of many rare species. Few of these had recolonized even after two years of more normal precipitation. Because these species are rare, it seems likely that plants that could serve as local seed sources will be rare, and thus that many of these species may be slow to recolonize plots, i.e., may be recruitment limited. At CCNHA, some late successional, native prairie species require 15 or more years to reach an abandoned field, and another 30 to 40 years to spread across the field (Tilman 1990). Thus extinctions imposed by periodic drought may limit diversity in prairie, with droughts leading to rapid local species loss, and recolonization leading to a slow reattainment of species richness. This drought-diversity cycle suggests that an increased frequency or intensity of drought should lead to decreased species richness.

Our results provide strong support for the hypothesized mechanism whereby environmental variation could limit biodiversity. During the drought of 1988, when aboveground living plant biomass fell to about half of its previous level, average species richness per plot was 37% lower than during pre-drought conditions (1982–1986). When all taxa were combined, rarer species had a much greater probability of being lost during the drought than abundant species (Fig. 5), just as expected (e.g., May and MacArthur 1972). Even when results were lumped over all plots of a treatment in four different fields (total species richness), about 20% of the species that had been present before the drought were absent in 1988, and few of these reappeared in 1989 or 1990 (Fig. 3C).

On a finer scale of resolution, the biomass fluctuation imposed by the drought was a selective agent of species loss. Annual grasses and forbs were more likely to be lost than perennials or than other taxa (mainly legumes and woody vines). Moreover, the probability that an annual grass or annual forb species would be lost from a habitat was independent of abundance (Fig. 5), whereas the loss rates of perennial grasses, perennial forbs, and other taxa decreased significantly with increased abundance.

Because drought had similar effects in completely unmanipulated natural vegetation (Treatment I), in plots receiving all nutrients other than nitrogen (Treatment A), and in other initially disturbed plots, the drought effects we observed may be quite general.

There are several potential explanations for the different loss rates observed for annuals and perennials. First, annuals may have avoided germination in the drought year, and may still be in the seed bank. Second, if biomass per individual is a more important determinant of the probability of death from drought than species abundance (biomass per m², as used in Fig. 5), then annuals, which start growth each year from seed, should have higher loss rates than established perennials. Third, an established perennial plant may experience a moister environment than an annual because the perennial's roots can tap deeper soil moisture reserves. Fourth, our annuals are all C-3 species, mostly of European origin, and may be more drought sensitive than native C-4 perennials.

There is no evidence that the drought of 1988 led to the global extinction of any species. Global extinction requires the local extinction of a species in all localities in which it occurs. Almost all the species in our sampled plots have wide geographic distributions, and are still present in localized areas within our fields, such as in more low-lying moister areas.

It could be argued that there were no true species losses in these plots, but that the species absent in 1988 were merely remaining in the soil in a dormant state until the return of more normal climatic conditions. This may apply to many of the annual species which have dormant seeds in the seed bank. However, if lost species were in a dormant state during the drought of 1988, they must

have remained in this dormant state in 1989, despite its more normal precipitation, and in 1990, which had above-normal precipitation (Fig. 2A). Indeed, the most surprising aspect of this study is not the loss of rare species during a harsh year, but the lack of a recovery in species richness during the following years when total community biomass had recovered (Fig. 2C). The slow recovery after the drought suggests that local species richness in these grasslands is recruitment limited.

Sampling theory predicts that a decline in species richness should occur when total community biomass declines. The magnitude of this effect is reflected in the biomass analog of the species-area curve (e.g., MacArthur and Wilson 1967):

$$S = cB^z$$

where S is species richness, c is a constant, B is total biomass sampled, and z an exponent. Most reported z values range from 0.1 to 0.3 (Connor and McCoy 1979, Robinson and Quinn 1988). Even with the largest of these z values, the 50% decline in total biomass observed during 1988 should have led to only a 19% reduction in species richness, whereas there was actually a 37% decline. Moreover, on average, there was only a 2.6% increase in species richness per plot from 1988 to 1989, despite the 100% increase in total biomass. This strongly suggests that there was a true loss of species during the drought that is not simply explained as a sampling artifact. The z value of 0.5 required to explain the loss of 37% of the species in 1988 would also predict their immediate return in 1989 when biomass returned to normal.

In total, our results demonstrate that a climatically harsh period can lead to significant reductions in local species richness, mainly by increasing the rate of local extinction of rare species. This suggests that climatic fluctuations may be one of the factors limiting the diversity of terrestrial plant communities. It is likely that each distinct type of environmental fluctuation will lead to the selective loss of certain taxa, but that, in general, population fluctuations will lead to greater extinction rates for rarer species.

These results are of potential relevance to the conservation of biodiversity. They suggest that increased drought frequency, which may accompany global climatic change, could be a threat to the preservation of rare species. Clearly, habitat destruction associated with agriculture and forestry is the major cause of the loss of biodiversity (e.g., papers in Wilson 1988). However, a change to a harsher or more variable climate may compound the problem of habitat destruction by decreasing the ability of rarer species to survive in the remnants of their original habitats.

Acknowledgements. We thank Connie Osbeck and numerous undergraduate summer field assistants for their help in sampling, Greg Spoden and Jim Zandlo of the State of Minnesota Climatology Office for providing climatic data, Eville Gorham, David Wedin and anonymous reviewers for comments on this manuscript, and the National Science Foundation (NSF/BSR 8811884) and the Andrew Mellon Foundation for financial support.

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