



Relationships between diversity and compositional stability in experimental grassland communities exposed to drought stress

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Abstract: Artificial grassland plots with various degrees of diversity were established near Heishiding Nature Reserve, Guangdong Province, China. After an establishment phase of one year, one half of each plot was exposed to drought stress in order to explore the relationship between diversity and compositional stability of the grassland communities. The experiment showed that relationships between diversity and compositional stability varied with the diversity values in non-stressed control subplots and the duration of drought disturbance. When control subplots had higher evenness, species richness negatively affected compositional stability, which led to a negative relationship between diversity and compositional stability. When control subplots had lower evenness, compositional stability was determined by evenness or species identity (particular species) at different periods of drought disturbance. This resulted in negative, weakly positive or no relationships between diversity and compositional stability. Based on these results, we suggest that different relationships between diversity and compositional stability, and controversial data from such relationships in previous studies may reflect differences in environmental and experimental conditions.

Introduction

The hypothesis that greater diversity leads to greater stability of species communities has been the matter of interest and debate for many decades (Tilman 1996, Pfisterer and Schmid 2002, Tilman et al. 2006, Ives and Carpenter 2007). With increasing diversity, greater stability has been correlated with an increased probability of species (or functional groups) that can adequately compensate for species harmed by disturbance (Tilman and Downing 1994, Tilman 1996, Naeem and Li 1997). In this view, a higher degree of compensation means greater instability of community composition (Tilman et al. 2006).

In previous studies, relationships between diversity and compositional stability exhibited different patterns. Frank and McNaughton (1991) reported a positive relationship between diversity and compositional stability in grassland communities of Yellowstone National Park, USA. In contrast, other theoretical and field studies reported negative relationships between diversity and compositional stability (Mellinger and McNaughton 1975, McNaughton 1977, Tilman 1996, Sankaran and McNaughton 1999, Lehman and Tilman 2000, Foster et al. 2002). Explanations for these negative relationships were controversial, however. Some studies attributed the negative relationship to the impact of species richness, i.e., compensatory responses among species in response to disturbance could lead to a negative relationship (Tilman 1996, Lehman and Tilman 2000). Other studies attributed the negative relationship to the impact of species identity (particular species) (McNaughton 1977, Sankaran and McNaughton 1999, Foster et al. 2002). Whether species

richness or species identity controls the relationship between diversity and compositional stability remained an open question. Furthermore, King and Pimm (1983) hypothesized that evenness of communities could have an impact on the relationship between diversity and compositional stability. This hypothesis has not been tested so far.

The relationship between diversity and compositional stability of plant communities has been studied with respect to many types of disturbance. Stress factors included burning (Sankaran and McNaughton 1999), grazing (Sankaran and McNaughton 1999), disruption of soil (Foster et al. 2002), and drought stress (Frank and McNaughton 1991, Rodríguez and Gómez-Sal 1994). The relationships between diversity and compositional stability were investigated at a single time point in these studies. However, Ives and Carpenter (2007) proposed that the consequence of diversity on compositional stability of communities could be more dynamically understood in the context of environmental changes. Drought strongly reduces biomass production of many plant communities (Herbel et al. 1972, Noy-Meir 1973, Tilman and Downing 1994, Briggs and Knapp 1995) and this often leads to significant changes in species composition (Torsell 1976, Tilman and El Haddi 1992, Fotelli et al. 2001). Global climate change is predicted to increase the frequency and intensity of high temperatures and drought in many regions (Easterling et al. 2000, Hoerling and Kumar 2003). Therefore, exploring relationships between diversity and compositional stability in the context of increasing drought has an important impact on ecosystem management and biodiversity conservation.

In the present study, we established experimental grassland plots with different degrees of diversity and exposed half of each plot to a drought stress. The resistance of a given grassland community to change the relative abundance of species in response to drought disturbance (Sankaran and McNaughton 1999, Foster et al. 2002) was used as a measure to estimate the compositional stability of the community. Unlike previous experiments, we examined relationships between diversity and compositional stability at different time points. The objective of the study was to examine whether relationships between diversity and compositional stability are constant or exhibit different patterns depending on the duration of drought disturbance. We also explored the impact of species richness and species identity on these relationships.

Materials and methods

Study site

The experimental site (23°33'17.69N, 111°48'05.70E) was established near Heishiding Nature Reserve, Guangdong Province, China. Site characteristics have been reported in Yu et al. (2000). To prepare the planting area, an arable field was completely burned in December 2003. An upper 10–15 cm of soil was removed to avoid germination of seeds from the burned field site (elimination of the seed bank). Seeds were planted on the resulting homogeneous substrate. The area was fenced to exclude mammalian herbivores.

Experimental design

357 Plots, each 4 m × 2 m, with 1-m walkways, were randomly assigned and planted with 1, 2, 4, 6, 8, 10, 15, 20, 25, 30, 35 or 40 plant species in April 2004. Seeds from all species used in the experiment were collected in the Heishiding Nature Reserve. Unwanted species were not removed during this establishment phase. Such a treatment could have disturbing effects on plant communities (Huston et al. 2000). Thus, some plots lost some species, while others were occasionally invaded by other species (Table 1).

Detailed methods and description of the experimental drought treatment have been reported in Wang et al. (2007). Briefly, in June 25, 2005, after an establishment phase of one year, each of the 357 plots was divided equally into two 2 m × 2 m subplots. One plot was left under unperturbed conditions (control subplot without drought stress treatment). The other subplot was exposed to an experimental drought stress treatment (drought subplot). Aboveground biomass of subplots was harvested at three time points: two months (August 25, 2005), four months (October 25, 2005) and one year (June 25, 2006) after the initiation of the drought stress treatment (hereafter referred to as 'T_{two months}', 'T_{four months}' and 'T_{one year}'). Aboveground vegetation in each subplot was sampled by clipping a 30 cm × 200 cm strip at the soil surface. All aboveground plant biomass (living vascular plants) was sorted to species, dried and then separately weighed. A

Table 1. Species used in the experiment. Seeds from 82 species (1-82) were planted at the beginning of the experiment. Planted species that disappeared during the establishment phase are marked by an asterisk. Colonized species (83-91) that spontaneously invaded (or derived from the seed bank of the test plot) are marked by two asterisks. Forbs are abbreviated by "f", shrubs by "s", legumes by "l", and grasses by "g".

Species	
1. <i>Hemistepta lyrata</i> (f)	47. <i>Vitex negundo</i> (s)
2. <i>Bidens pilosa</i> (f)	48. <i>Hedyotis auricularia</i> (f)
3. <i>Siegesbeckia orientalis</i> (f)*	49. <i>Agrimonia pilosa</i> (f)
4. <i>Xanthium sibiricum</i> (f)	50. <i>Melastoma affine</i> (s)*
5. <i>Eupatorium chinense</i> (f)	51. <i>Dichondra repens</i> (f)*
6. <i>Elephantopus scaber</i> (f)	52. <i>Euphorbia hirta</i> (f)
7. <i>Inula cappa</i> (s)	53. <i>Cuphea hookeriana</i> (f)
8. <i>Artemisia japonica</i> (f)	54. <i>Medicago sativa</i> (l)*
9. <i>Conyza canadensis</i> (f)	55. <i>Indigofera amblyantha</i> (l)
10. <i>Synedrella nodiflora</i> (f)*	56. <i>Cassia mimosoides</i> (l)
11. <i>Ageratum conyzoides</i> (f)	57. <i>Crotalaria mucronata</i> (l)
12. <i>Kalimeris indica</i> (f)*	58. <i>Desmodium velutinum</i> (l)
13. <i>Cichorium intybus</i> (f)	59. <i>Cassia tora</i> (l)
14. <i>Gynura crepidioides</i> (f)*	60. <i>Cassia occidentalis</i> (l)
15. <i>Ageratum housetonianum</i> (f)	61. <i>Lespedeza cuneata</i> (l)
16. <i>Artemisia verlotorum</i> (f)*	62. <i>Desmodium pulchellum</i> (l)
17. <i>Artemisia lavandulaefolia</i> (f)*	63. <i>Desmodium triquetrum</i> (l)
18. <i>Perilla frutescens</i> (f)*	64. <i>Uraria lagopodioides</i> (l)
19. <i>Anisomeles indica</i> (f)	65. <i>Eragrostis curvula</i> (g)*
20. <i>Elysiopsis ciliate</i> (f)*	66. <i>Paspalum distichum</i> (g)*
21. <i>Elysiopsis argyri</i> (f)	67. <i>Sorghum sudanense</i> (g)
22. <i>Keiskea australis</i> (f)*	68. <i>Echinochloa oryzoides</i> (g)
23. <i>Orthodon diantherus</i> (f)	69. <i>Digitaria sanguinalis</i> (g)*
24. <i>Achyranthes aspera</i> (f)	70. <i>Coix lacryma-jobi</i> (g)
25. <i>Celosia argentea</i> (f)	71. <i>Lophatherum gracile</i> (g)
26. <i>Celosia cristata</i> (f)*	72. <i>Pennisetum alopecuroides</i> (g)
27. <i>Amaranthus lividus</i> (f)*	73. <i>Paspalum thunbergii</i> (g)
28. <i>Amaranthus spinosus</i> (f)	74. <i>Eleusine indica</i> (g)
29. <i>Malvastrum coromandelianum</i> (f)	75. <i>Dactyloctenium aegyptiacum</i> (g)
30. <i>Abelmoschus manihot</i> (f)	76. <i>Sporobolus indicus</i> (g)*
31. <i>Sida rhombifolia</i> (s)	77. <i>Miscanthus floridulus</i> (g)
32. <i>Urena lobata</i> (s)	78. <i>Cynodon dactylon</i> (g)
33. <i>Abutilon indicum</i> (f)*	79. <i>Setaria palmifolia</i> (g)
34. <i>Triumfetta bartramia</i> (s)	80. <i>Scleria biflora</i> (g)*
35. <i>Triumfetta tomentosa</i> (s)	81. <i>Gahnia tristic</i> (g)
36. <i>Triumfetta annua</i> (s)	82. <i>Cyperus exaltatus</i> (g)
37. <i>Corchorus capsularis</i> (s)	83. <i>Conyza canadensis</i> (f)**
38. <i>Ludwigia prostrata</i> (f)	84. <i>Phyllanthus urinaria</i> (f)**
39. <i>Ludwigia caryophylla</i> (f)	85. <i>Artemisia argyri</i> (f)**
40. <i>Helicteres angustifolia</i> (f)	86. <i>Desmodium styracifolium</i> (s)**
41. <i>Melochia corchorifolia</i> (f)*	87. <i>Imperata cylindrica</i> (g)**
42. <i>Adenosma glutinosum</i> (f)*	88. <i>Herba Hedyotis</i> (f)**
43. <i>Scoparia dulcis</i> (f)	89. <i>Monochoria vaginalis</i> (f)**
44. <i>Plantago asiatica</i> (f)	90. <i>Eragrostis unioides</i> (g)**
45. <i>Chenopodium ambrosioides</i> (f)	91. <i>Setaria viridis</i> (g)**
46. <i>Polygonum hydropiper</i> (f)*	

different portion of each subplot was sampled at the three times of harvest.

Diversity index

The Shannon diversity index (H) has been used in many previous field studies to explore relationships between diversity and compositional stability of grassland communities (Foster et al. 2002). H was calculated as follows (Shannon 1948):

$$H = - \sum_{i=1}^S p_i \ln p_i \quad (1)$$

where p_i represents the proportional contribution of species to community biomass, and S (species richness) is the number of the species that appeared in the control subplot. The H values of control subplots were determined at various time points (two months, four months and one year) after initiation of the drought stress treatment (hereafter referred to as ' $H_{\text{two months}}$ ', ' $H_{\text{four months}}$ ' and ' $H_{\text{one year}}$ ') to reflect the gradient of diversity in plots under control conditions.

Evenness (E) was calculated according to the formula proposed by Pielou (1975):

$$E = H/\ln S \quad (2)$$

Compositional stability

The similarity index (SI) modified from the dissimilarity index (Bray and Curtis 1957), was calculated using data from each subplot pair (of a given plot) in order to reflect the resistance to changes in community structure:

$$SI = 1 - \frac{1}{2} \sum_{i=1}^m |x^i - x'^i| \quad (3)$$

where x^i and x'^i are the relative abundances of species i in control subplots, and subplots exposed to drought stress, respectively. m is the total number of species of a given plot (species observed in control and drought subplots). It is assumed that SI is an appropriate measure for compositional stability of a grassland community. If SI is zero, no species are identical, indicating maximal changes in relative abundances of species in response to the drought stress treatment (low degree of resistance); if SI is one, all species are identical in both subplots and appear with same relative abundances, i.e., there are no changes in relative abundances of species in response to drought disturbance (high degree of resistance).

Data analysis

To examine the relationship between diversity and compositional stability, we used simple regressions to analyze the dependence of the similarity index (SI) from the Shannon index (H). Simple regression analysis was also used to estimate the dependence of SI from species richness (S) and evenness (E), respectively.

The relative growth rate (RGR) of species (Connolly and Wayne 2005), which is a measure for the proportional rate of growth of a given species, reflects changes in biomass production of a given species during an experimental period. We used RGR to express the changes in biomass production of dominant species in response to drought disturbance (the dominant species of a plot was defined as the species that showed highest accumulation of biomass in the control subplot):

$$RGR = \ln(B_{\text{drought}}/B_{\text{control}}) / t$$

where B_{drought} is the biomass of the dominant species in drought subplots, B_{control} is the biomass of the dominant spe-

cies in control subplots, t (unit: month) is the duration of the experiment and \ln is the natural logarithm. Dominant species in control subplots were identified at $T_{\text{two months}}$, $T_{\text{four months}}$ and $T_{\text{one year}}$, and their corresponding RGR calculated (hereafter referred to as ' $RGR_{\text{two months}}$ ', ' $RGR_{\text{four months}}$ ' and ' $RGR_{\text{one year}}$ '). Linear and non-linear regressions were used to analyze the relationship between SI and RGR of dominant species.

After the one-year establishment phase, four species (*Triumfetta bartramia*, *Gahnia tristis*, *Ageratum houstonianum* and *Hemistepta lyrata*) were highly competitive. Most plots were also dominated by these four species two months after initiation of the experiment (at $T_{\text{two months}}$). These plots were classified according to their dominant species into the following four categories: *Triumfetta bartramia* plots, *Gahnia tristis* plots, *Ageratum houstonianum* plots and *Hemistepta lyrata* plots. The differences of SI among the four types of plots were tested by one-way ANOVA (LSD test) at $P < 0.05$ level for each experimental phase in order to reflect the effect of species identity (particular species) on compositional stability.

Correlations were conducted using the Pearson correlation analysis. Differences of evenness in control subplots between the three experimental phases were analyzed by using paired- t tests. All statistical analyses were performed with the SPSS 10.0 program for Windows.

Results

The relationships between diversity and compositional stability were compared after different periods of drought stress. Using simple regression analysis, we explored relationships between the similarity index of a subplot pair (SI , a measure for compositional stability of a community) and the Shannon index (H) from the control subplot. Data were collected for each experimental phase. On 25 August 2005, two months after initiation of the drought stress, $SI_{\text{two months}}$ was negatively correlated with $H_{\text{two months}}$, i.e., the Shannon index in the 2 m² area of the control subplot (Fig. 1A). On 25 October 2005, i.e., when drought stress continued for four months, $SI_{\text{four months}}$ decreased significantly with increasing $H_{\text{two months}}$ and $H_{\text{four months}}$, respectively (Fig. 1B and C). After one year of drought stress, there was no relationship between $SI_{\text{one year}}$ and $H_{\text{two months}}$ (Fig. 1D), but $SI_{\text{one year}}$ was weakly positively correlated with $H_{\text{four months}}$ and significantly negatively correlated with $H_{\text{one year}}$ (Fig. 1E and F). These different patterns indicate that the relationships between diversity and compositional stability were not constant, but varied depending on the degree of diversity in control subplots and the duration of drought disturbance.

As commonly defined, H depends on species richness (SR , the number of plant species in a community) and on species evenness (E , a measure of how abundances are distributed among species) (Peet 1974), which was determined for control subplots in this study. We separated the two factors and analyzed their individual effects on compositional stability. There were significant negative effects of $E_{\text{two months}}$ on

$SI_{two\ months}$ ($r = -0.342$, $n = 357$, $P < 0.001$). $E_{two\ months}$ and $E_{four\ months}$ both negatively correlated with $SI_{four\ months}$ ($r = -0.241$ and $r = -0.250$, respectively; $n = 357$, $P < 0.001$ for both). These relationships are similar to those between H and SI . However, a negative effect of E ($E_{two\ months}$, $E_{four\ months}$ and $E_{one\ year}$) on $SI_{one\ year}$ was not seen ($P > 0.05$ for all). $SR_{two\ months}$ also had no significant effects on SI at all three experimental phases ($P > 0.05$ for all). Furthermore, no significant effects of $SR_{four\ months}$ on $SI_{four\ months}$ and $SI_{one\ year}$ were found ($P > 0.05$ for both). However, $SI_{one\ year}$ negatively depended on the effects of $SR_{one\ year}$ ($r = -0.302$, $n = 357$, $P < 0.001$). These data suggest that relationships between diversity and compositional stability may be controlled by mechanisms related to evenness or species richness,

which varied with the degree of diversity in control subplots and the duration of drought disturbance.

In control subplots at all three experimental phases, $E_{one\ year}$ was significantly higher than $E_{two\ months}$ and $E_{four\ months}$ ($t = 6.123$ and $t = 5.476$, respectively; $n = 357$, $P < 0.0001$ for both). In control subplots with lower evenness (at $T_{two\ months}$ and $T_{four\ months}$), a significant nonlinear reduction was found for SI , as the relative growth rate (RGR) of dominant species decreased (Fig. 2A, B). When control subplots had higher evenness, no significant relationship between RGR of dominant species and SI was seen at $T_{one\ year}$ (Fig. 2C). Hence, when evenness was low (and dominance high), changes in biomass accumulation of dominant species in response to drought disturbance seemed to influence the compositional

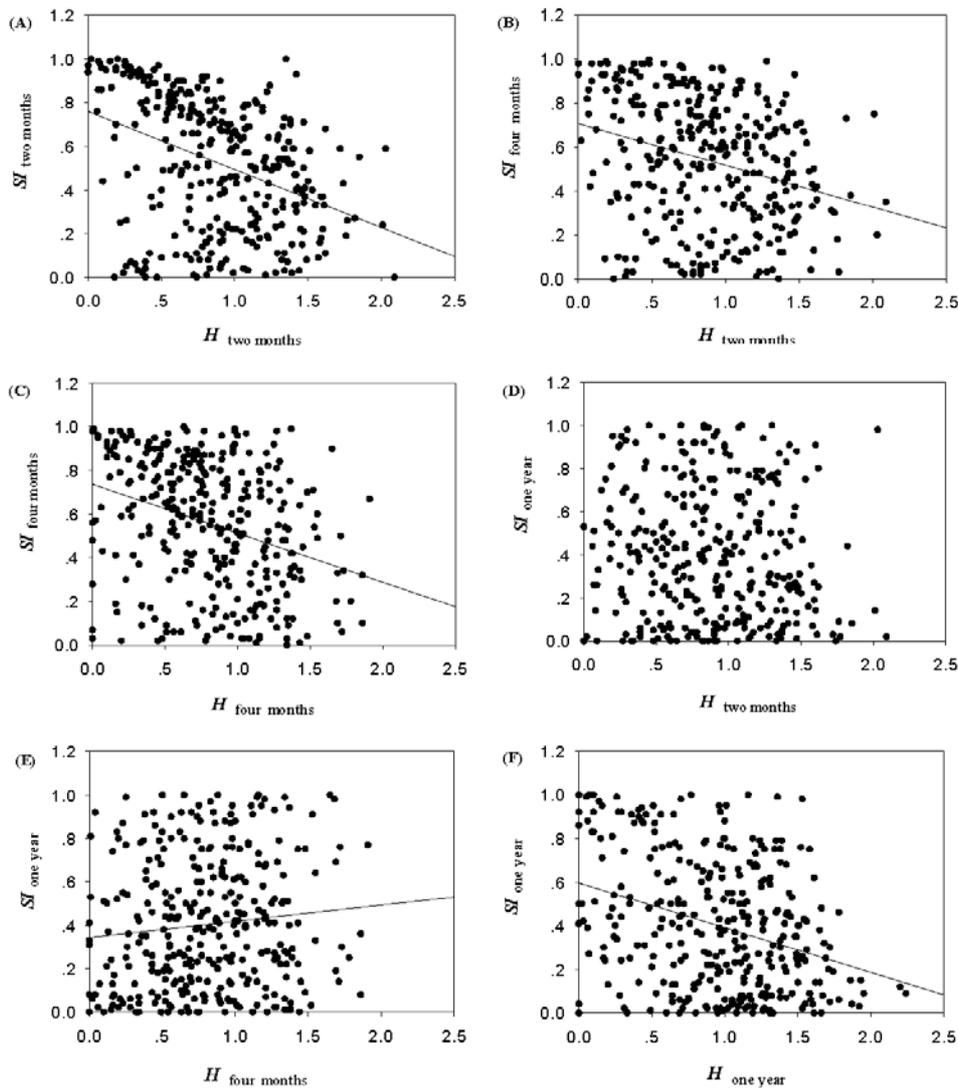


Figure 1. Relationship between similarity index (SI) and Shannon index (H) at different experimental phases. $H_{two\ months}$, $H_{four\ months}$ and $H_{one\ year}$ represent the diversity in control subplots at the indicated time point (drought stress for two months, four months and one year, respectively). (A) Relationship between $SI_{two\ months}$ and $H_{two\ months}$ ($r = -0.338$, $n = 357$, $P < 0.001$). (B) Relationship between $SI_{four\ months}$ and $H_{two\ months}$ ($r = -0.205$, $n = 357$, $P < 0.001$). (C) Relationship between $SI_{four\ months}$ and $H_{four\ months}$ ($r = -0.325$, $n = 357$, $P < 0.001$). (D) Relationship between $SI_{one\ year}$ and $H_{two\ months}$ ($P = 0.328$). (E) Relationship between $SI_{one\ year}$ and $H_{four\ months}$ ($r = 0.106$, $n = 357$, $P = 0.052$). (F) Relationship between $SI_{one\ year}$ and $H_{one\ year}$ ($r = -0.333$, $n = 357$, $P < 0.001$).

Table 2. Differences in similarity index (*SI*) values among four plot categories (plots dominated by *Triumfetta bartramia*, *Gahnia tristis*, *Ageratum houstonianum* and *Hemistepta lyrata*, respectively). One-way ANOVA (LSD test at $P < 0.05$ level) was used to estimate significant differences of *SI* among the four plot categories. Values given are means \pm SE.

	T _{two months}	T _{four months}	T _{one year}
<i>Triumfetta bartramia</i>	0.528 \pm 0.098a [†]	0.524 \pm 0.088a	0.504 \pm 0.056ab
<i>Gahnia tristis</i>	0.532 \pm 0.084a	0.530 \pm 0.079a	0.520 \pm 0.041a
<i>Ageratum houstonianum</i>	0.524 \pm 0.092a	0.526 \pm 0.087a	0.439 \pm 0.065b
<i>Hemistepta lyrata</i>	0.538 \pm 0.045a	0.531 \pm 0.042a	0.336 \pm 0.029c

[†] Means followed by the same letters within a line are not significantly different ($P > 0.05$).

stability of the experimental grassland communities. The more dominant species were inhibited by drought, the less stable was the composition of the plots. However, changes in biomass accumulation of dominant species had little influence on the compositional stability of grassland communities when evenness was high (and dominance low).

The effect of species identity (particular species) on compositional stability was investigated for four categories of plots, which were dominated by *Triumfetta bartramia*, *Gahnia tristis*, *Ageratum houstonianum* and *Hemistepta lyrata*, respectively. The results showed that the species identity did not influence the compositional stability at T_{two months} and T_{four months} as *SI* values displayed no significant differences ($P > 0.05$ for T_{two months} and T_{four months}) among these four plot categories (Table 2). A significant difference ($F_{3, 262} = 4.234, P = 0.006$) was found at T_{one year}, however (Table 2). These results indicate that species identity may have an important effect on compositional stability of grassland communities exposed to persistent drought (drought stress for one year).

Discussion

In this study, we explored relationships between diversity (*H*) and compositional stability (*SI*) of artificial grassland communities exposed to different periods of drought stress. Based on simple regression analysis, we found that relationships between diversity and compositional stability

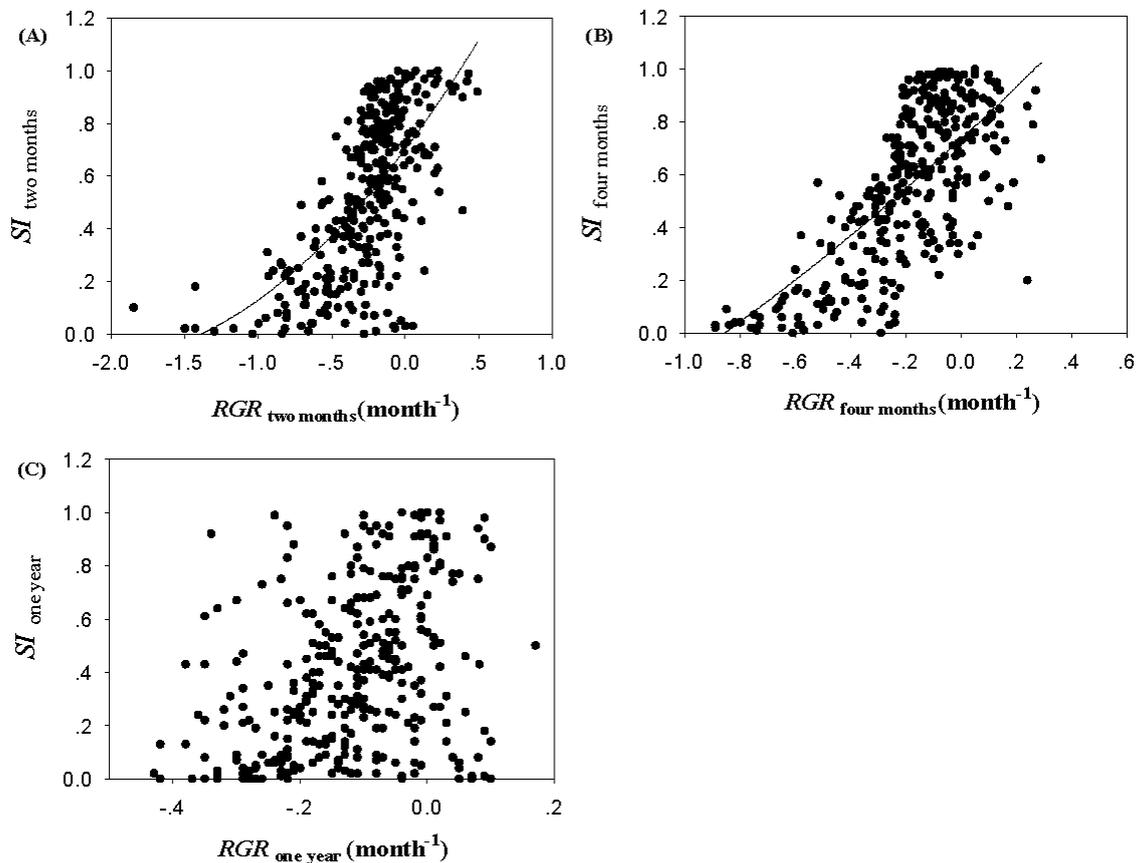


Figure 2. Relationship between similarity index (*SI*) and relative growth rate (*RGR*) of dominant species (the species that accumulated most biomass in control subplots) at three different experimental phases. Dominant species of plots were identified at T_{two months}, T_{four months} and T_{one year}, respectively. Relative growth rates (*RGR*) of dominant species at these time points are indicated as '*RGR_{two months}*', '*RGR_{four months}*' and '*RGR_{one year}*'. Lines represent fitted quadratic curves using nonlinear regressions. (A) Relationship between *SI* and *RGR_{two months}* at T_{two months} (fitted line: $y = 0.171x^2 + 0.746x + 0.704, R^2 = 0.487, n = 357, P < 0.001$). (B) Relationship between *SI* and *RGR_{four months}* at T_{four months} (fitted line: $y = 0.123x^2 + 0.964x + 0.735, R^2 = 0.497, n = 357, P < 0.001$). (C) Relationship between *SI* and *RGR_{one year}* at T_{one year} ($P > 0.05$).

were not constant, but varied with diversity in control subplots and duration of drought disturbance. In contrast to predictions of McNaughton (1977), Tilman (1996) and Lehman and Tilman (2000), we suggest that relationships between diversity and compositional stability may be controlled by evenness (E), species richness (SR) or species identity (particular species), which vary and depend on both, diversity in control subplots and duration of drought disturbance. Consequently, it is likely that factors controlling compositional stability of grassland communities are different under different environmental and experimental conditions, and thus lead to different relationships between diversity and compositional stability.

McNaughton (1977), Tilman (1996) and Lehman and Tilman (2000) predicted that negative relationships between diversity and compositional stability reflect a negative effect of species richness on compositional stability due to compensatory responses of species in response to disturbance. Negative relationships between H and SI were also found in this study. When the control subplots had higher evenness (at $T_{\text{one year}}$), $SR_{\text{one year}}$ also had a negative effect on SI , which led to the negative relationship between $H_{\text{one year}}$ and SI . However, when the control subplots had lower evenness (at $T_{\text{two months}}$ and $T_{\text{four months}}$), the observed negative relationships between H ($H_{\text{two months}}$ and $H_{\text{four months}}$) and SI were not influenced by effects of species richness. Consequently, we speculate that the predictions of McNaughton (1977), Tilman (1996) and Lehman and Tilman (2000) will occur in communities with high evenness values, as responses of individual species may have important effects on biomass composition, thereby promoting an even distribution of species abundance (Haper 1977, Wilsey and Potvin 2000, Polley et al 2003). However, typical natural communities often exhibit low evenness (Schwartz et al. 2000, Stirling and Wilsey 2001). Dominant species with a large abundance in natural communities usually play key roles in many ecosystems (Foster et al. 2002, Haddad et al. 2002, Smith and Knapp 2003, Emery 2007, Polley et al. 2007). Accordingly, responses of dominant species to drought stress in this study were associated with compositional stability, when control subplots had lower evenness values (at $T_{\text{two months}}$ and $T_{\text{four months}}$).

Whether species richness or species identity controls relationships between diversity and compositional stability has been debated in previous reports (McNaughton 1977, Tilman 1996, Sankaran and McNaughton 1999, Lehman and Tilman 2000, Foster et al. 2002). In this study, we provide evidence that species richness will control the relationship between diversity and compositional stability when control subplots have higher evenness values. In control subplots with lower evenness, the negative relationship between diversity and compositional stability at $T_{\text{two months}}$ and $T_{\text{four months}}$ seem to reflect the negative effects of E ($E_{\text{two months}}$ and $E_{\text{four months}}$) on compositional stability (SI). We predict that E affects SI by mechanisms related to growth of dominant species under drought stress conditions, as the increase in E significantly decreased the relative growth rate (RGR) of dominant species at $T_{\text{two months}}$ and $T_{\text{four months}}$ ($E_{\text{two months}}$ at $T_{\text{two months}}$: $r =$

-0.409 , $n = 357$, $P < 0.0001$; $E_{\text{two months}}$ at $T_{\text{four months}}$: $r = -0.415$, $n = 357$, $P < 0.0001$; $E_{\text{four months}}$ at $T_{\text{four months}}$: $r = -0.392$, $n = 357$, $P < 0.0001$; data not shown). Increases in E reflect a more even distribution of species abundances. This seems to be associated with increasing competitive effects of neighboring species on dominant species (Weiner 1982, Zamfir and Goldberg 2000, Wilson et al. 2003, Damato and Puettmann 2004), resulting in a RGR reduction of dominant species. However, the negative effects of E disappeared at $T_{\text{one year}}$ in our experimental grassland communities. This may be related to the strong effects of species identity (particular species) on compositional stability. Species identity may also affect SI by influencing growth responses of dominant species, as the RGR of four common dominant species exhibited a significant difference at $T_{\text{one year}}$ ($F_{3, 262} = 3.128$, $P < 0.05$; data not shown). Under strong abiotic stress conditions, competitive interactions among species may have less impact on community composition, because plant growth is then primarily limited by environmental conditions (Savile 1960, Billings and Mooney 1968, Grime 1977). Accordingly, plant traits that link responses of biomass production to environmental stress may control plant growth (Maestre et al. 2005, 2006, Haddad et al. 2008). Consequently, no or weakly positive relationships between H ($H_{\text{two months}}$ and $H_{\text{four months}}$) and SI at $T_{\text{one year}}$ may provide an explanation that species identity mainly controlled compositional stability in our experiment. Such an explanation could also be extended to other stress factors than drought. We suggest that the different patterns of relationships between H and SI , which have been controversially interpreted in previous studies (McNaughton 1977, Tilman 1996, Frank and McNaughton 1991, Rodríguez and Gómez-Sal 1994, Sankaran and McNaughton 1999, Lehman and Tilman 2000, Foster et al. 2002) reflect special cases of specific environmental and experimental conditions. With other words, ecological mechanisms affecting compositional stability will be different under different environmental and experimental conditions, and this will lead to different relationships between diversity and compositional stability.

The knowledge on relationships between diversity and compositional stability of grassland communities exposed to different periods of drought stress has implications for ecosystem management and biodiversity conservation. In natural communities, the biomass and number of individuals are almost never evenly distributed between species and many communities are dominated by one or a few species (Ugland and Gray 1982, Wilson et al. 1996, Weiher and Keddy 1999, Mulder et al. 2004, Mattingly et al. 2007). Therefore, besides endangered species, nature conservation should also consider protection of dominant key species, particularly in cases where the constancy of ecosystems and the compositional structure of communities should be maintained. Indeed, a greater understanding of the ecological link between species identity and compositional stability is required to predict the effects of diversity on compositional stability of communities under changing and extreme environmental conditions. Our data only reflect a situation where key spe-

cies responded “unfavorably” to experimental drought disturbance, but we hypothesize that the investigated relationships would be similar in the context of other environmental stress factors. In conclusion, the results of this study may have an important implication for future conservation and restoration of grassland communities, particularly in ecosystems with irregular drought periods.

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